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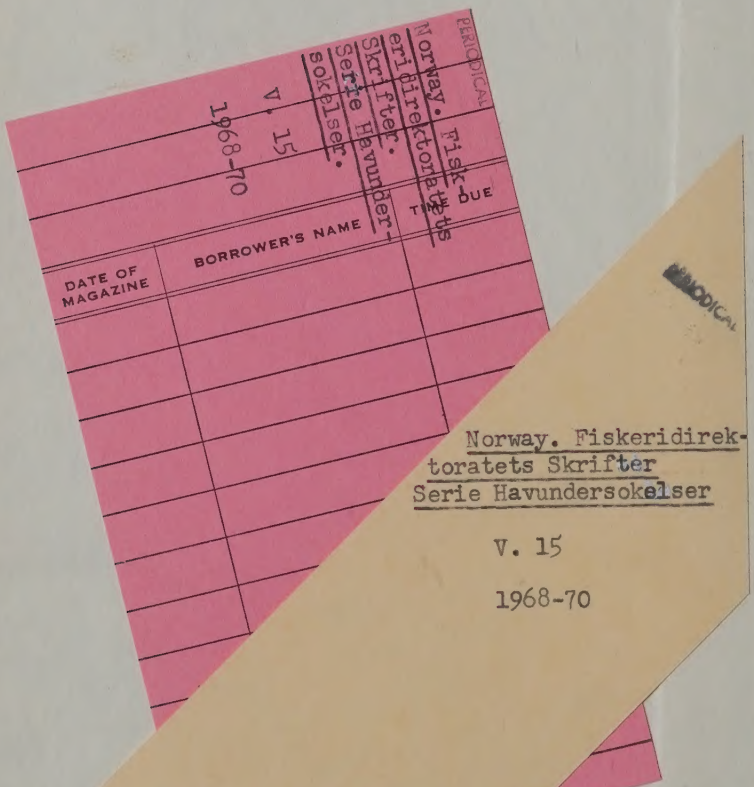

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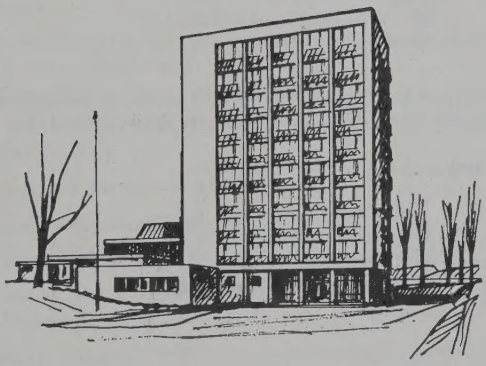

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CONTENTS

Pages

1968. No. 1. DEVOLD, FINN. The formation and the disappearance of a stock unit of Norwegian herring ..... 3—16

JAKOBSSON, JAKOB. Herring migrations east of Iceland during the summer and autumn 1966 and 1967 ..... 17—22

1969. No. 2. TVEITE, STEIN. Zooplankton and the discontinuity layer in relation to echo traces in the Oslofjord ..... 25—35

HARALDSVIK, STEINAR. The autumn spawning group of herring in the northeastern North Sea ..... 36—64

DANIELSSEN, DIDRIK S. Investigations on herring, *Clupea harengus* L., from the Norwegian Skagerak coast during the years 1963—64 ..... 65—82

NÆVDAL, GUNNAR. Studies on serum esterase in herring and sprat ..... 83—90

MØLLER, DAG and NÆVDAL, GUNNAR. Studies on hemoglobins of some gadoid fishes ..... 91—98

1969. No. 3. Contributions given in honour of Gunnar Rollefsen at his 70th birthday. Editors: Erling Bratberg, Erling Bakken, Odd Nakken ..... 99—379

Foreword. KLAUS SUNNANÅ ..... 103—107

The publications of GUNNAR ROLLEFSEN ..... 108—111

An appreciation. ARTHUR E. J. WENT ..... 112—113

Triumphs and frustrations of the fishery biologist. PIETER KORRINGA ..... 114—127

NÆVDAL, GUNNAR. Studies on blood proteins in herring ... 128—135

BARNES, HAROLD and BARNES, MARGARET. *Balanus balanoides* (L.) on the Atlantic coast of France: Further observations on the small isolated population at the southern limit of its distribution at Arcachon ..... 136—138

HOGNESTAD, PER T. Notes on Greenland halibut, *Reinhardtius hippoglossoides* (Walbaum), in the eastern Norwegian Sea 139—144

TEMPLEMAN, WILFRED. The scientific name, distribution and characteristics of the blue ling, *Molva dypterygia* (Pennant), from West Greenland and Newfoundland areas ..... 145—162

CARRUTHERS, JAMES N. The plastic seabed "oyster" for measuring bottom currents ..... 163—171

MATHISEN, OLE A. Growth of sockeye salmon in relation to abundance in the Kvichak district, Bristol Bay, Alaska 172—185

OLSEN, STEINAR. The halibut gillnet fishery in West Finnmark. Analysis of landings data from Øksfjord 1955—65 186—197

MARTY, JU. JU. On the problem of the effect of fisheries on fish stocks ..... 198—201

(Cont.)

Pages

LAEVASTU, TAIVO. Effects of ocean thermal structure on fish finding with sonar ..... 202—209

CRAIG, ROBERT E. and FORBES, SINCLAIR T. Design of a sonar for fish counting ..... 210—219

MØLLER, DAG. The relationship between Arctic and coastal cod in their immature stages illustrated by frequencies of genetic characters ..... 220—233

LIE, ULF. The logarithmic series and the lognormal distribution applied to benthic infauna from Puget Sound, Washington, USA ..... 234—245

SERGEANT, DAVID E. Feeding rates of cetacea ..... 246—258

NIKOLSKY, GEORGY V. Intraspecific structure and variability in relation to fisheries management ..... 259—265

DIETRICH, GÜNTER. Physical variability in the sea and the consequences for fisheries hydrography ..... 266—273

SUNDNES, GUNNAR, BRATLAND, PER and STRAND, ELSA. The gas content in the coregonid swimbladder ..... 274—278

TAMBS-LYCHE, HANS. Notes on the distribution and ecology of *Myxine glutinosa* L. ..... 279—284

LJØEN, RIKARD and NAKKEN, ODD. On the hydrography of the shelf waters off Møre and Helgeland ..... 285—294

SKUD, BERNARD E. The effect of fishing on size composition and sex ratio of offshore lobster stocks ..... 295—309

HUBBS, CARL L. and TAYLOR, LEIGHTON R. JR. Data on life history and characters of *Galeus piperatus*, a dwarf shark of Golfo de California ..... 310—330

DANIELSSEN, DIDRIK S. On the migrations of the cod in the Skagerak shown by tagging experiments in the period 1954—1965 ..... 331—338

BERGE, GRIM. Predicted effects of fertilizers upon the algae production in Fern Lake ..... 339—355

MCHUGH, JOHN L. Comparison of Pacific sardine and Atlantic menhaden fisheries ..... 356—367

CUSHING, DAVID H. The fluctuation of year-classes and the regulation of fisheries ..... 368—379

1970. No. 4. DRAGESUND, OLAV. Factors influencing year-class strength of Norwegian spring spawning herring (*Clupea harengus* Linné) ..... 381—450

DRAGESUND, OLAV. Distribution, abundance and mortality of young and adolescent Norwegian spring spawning herring (*Clupea harengus* Linné) in relation to subsequent year-class strength ..... 451—554

1970. No. 5. NÆVDAL, GUNNAR. Further studies on blood protein polymorphism in sprat ..... 555—564

NÆVDAL, GUNNAR. Distributions of multiple forms of lactate dehydrogenase, aspartate aminotransferase and serum esterase in herring from Norwegian waters ..... 565—572

NÆVDAL, GUNNAR. Studies on blood proteins of mackerel .. 573—583

FiskDir. Skr. Ser. HavUnders., *15*: 1—22.

THE FORMATION AND THE DISAPPEARANCE OF A STOCK UNIT OF NORWEGIAN HERRING

By

Finn Devold

Institute of marine research, Bergen

With a section on herring migrations east of Iceland by

Jakob Jakobsson.

THE FORMATION AND THE DISAPPEARANCE OF A STOCK UNIT OF NORWEGIAN HERRING

By

Finn Devold

Institute of Marine Research, Bergen

INTRODUCTION

About 100 years ago great schools of socalled «large herring» migrated to northern Norway. Very good descriptions of this migration are published in «Norges Fiskerier» from 1868—1874. The herring were mature herring coming from the north, migrating southwards along the coast. The schools were discovered because they were followed by flocks of whales and thousands of birds. In many cases the schools went into shallow areas where thousands of barrels could be filled with herring caught even by means of dip nets. The main gears used during the fisheries were however, beach seines and tangle nets.

In 1868 the herring arrived in the coastal area of Vesterålen in the middle of October, and in 1874, the last year it showed up, as early as September 17th. Since 1875 only young immature herring have formed the basis of the herring fisheries in northern Norway.

Sven Runnstrøm (1936) reported that mature herring were caught in the Andenes area in 1935, and Russian investigators found herring larvae between Røst and Sørøya in 1938. These herring were regarded as belonging to a special unit of herring which they called «Murman herring» (Manteifel and Marty 1939).

In the present century no commercial fisheries of economic importance were carried out by Norwegian ships on mature herring off northern Norway before late March 1958, when R/V «G. O. Sars» discovered schools of herring spawning in the Røst area (G. Sætersdal, verbal inf.). Several Norwegian purse seiners, which were on their way home after the winter herring fishery in the Møre area, went to the Røst Bank and caught about 70 000 hl of herring before the schools disappeared in the middle of April. The herring constituted of the extremely strong 1950 year-class.

Since the winter 1950-51 a Norwegian research ship has followed the herring schools on their spawning migration from the wintering area east of Iceland to the spawning grounds along the Norwegian coast. In 1959 also the northern area was investigated with regard to spaw-

ning migration of herring to the Lofoten area, but with negative results. During the years 1960—62 the northern area was carefully investigated before and during the Lofoten cod season, but mature herring were not located.

From these previous investigations it can be concluded that mature herring occasionally have appeared off northern Norway also in this century. The years of appearance were when very strong year-classes of the Norwegian winter herring recruited the mature stock. In the years 1935—38 the 1930 year-class and in 1958 the 1950 year-class were dominating the northern unit.

According to the author's explanation of the periodicity of the appearance of the Atlanto-Scandian herring in Scandinavian coastal waters (Devold 1963 a), the wintering and spawning of the main part of the Norwegian winter herring is sooner or later to be expected off northern Norway. When therefore many schools of mature herring on February 2nd, were discovered by R/V « G. O. Sars» off Finnmark at the same time as the main part of the winter herring were following it's wellknown route from the wintering area east of Iceland to the spawning grounds off Møre, it was considered important to follow the further migrations of the northern unit.

MATERIAL AND METHODS

The consentrations of the northern unit of the mature herring have been located with sonar and echo-sounders by the Norwegian research vessels and by hired ships through the years 1963—66. The size of the stocks has been estimated from echo-recordings and from commercial catches.

Samples secured from the herring schools were as usual analysed with regard to sex, length, weight, age, stage of gonades etc.

RESULTS

THE 1963—SITUATION

On February 2nd 1963, R/V «G. O. Sars» located many schools of herring in the area from North Cape to Sørøya (S. Olsen, verbal inf.). Samples taken with trawl, showed a mixture of mature and immature herring. The sampled herring belonged mainly to the 1959 year-class which seemed to be very abundant. 20 % were in maturity stage IV.

On March 20th the herring were discovered off Røst and disappeared in early April. These herring were a mixture of spawning and immature herring belonging to the 1959 and 1960 year-class.

On July 11th 1963 the R/V «Johan Hjort» located herring schools in position N 68°05' E 10°08'. From this position on a direct course of 72 degrees schools of herring were located over a distance of about 50 miles. The findings were broadcasted and a few Norwegian purse seiners gathered in the area and made good catches until the middle of August, when the fishermen lost contact with the herring schools. Samples were not secured from these schools, but according to information from fishermen and from reduction plants, the herring had about the same length distribution as the herring which had been caught in late March and early April on the Røst Bank (Devold 1963 b).

On September 25th 1963 schools of herring were discovered about 50 miles north of Torsvåg by the R/V «G. O. Sars». Samples showed a mixture of mature herring and immature fat herring from the year-classes 1959 and 1960. The schools stayed near the bottom during day and approached the surface in the evening (Dragesund 1964).

The herring schools moved eastward during October and gathered in the Ingøy Deep to the north of Hammerfest in late October and stayed on there in November—December. The vertical migration of the herring schools to the surface layer in the evening ceased during November, and the herring kept later to the cold bottom water day and night.

From October 20th to November 3rd the coastal area between Lofoten and North Cape were investigated by R/V «Johan Hjort» (Devold 1964 a). Great consentrations of mature herring were located in the Ingøy Deep during this cruise, but no herring of the year-classes 1959—61 were located outside this area.

R/V «Asterias» located the herring in the Ingøy Deep several times during the autumn of 1963 (Hognestad 1964). The Norwegian R/V «Thor Iversen» followed the movements of the herring schools in the Ingey Deep and secured samples with a pelagic trawl. The herring were in this way under constant observation. Fig. 1 shows the most likely movement of this herring through the year 1963.

THE 1964—SITUATION

During late January 1964 the herring schools disappeared from the Ingøy Deep. When R/V «Johan Hjort» was available, the ship went to northern Norway to look for the disappeared herring.

On February 29th many herring schools were located about 10 miles north of Røst and in a northeasterly direction from this position or about 30 miles (Devold 1964 a).

The herring schools migrated to the Røst Bank and the Vestfjord. Information to the fishermen about the movements of the schools were

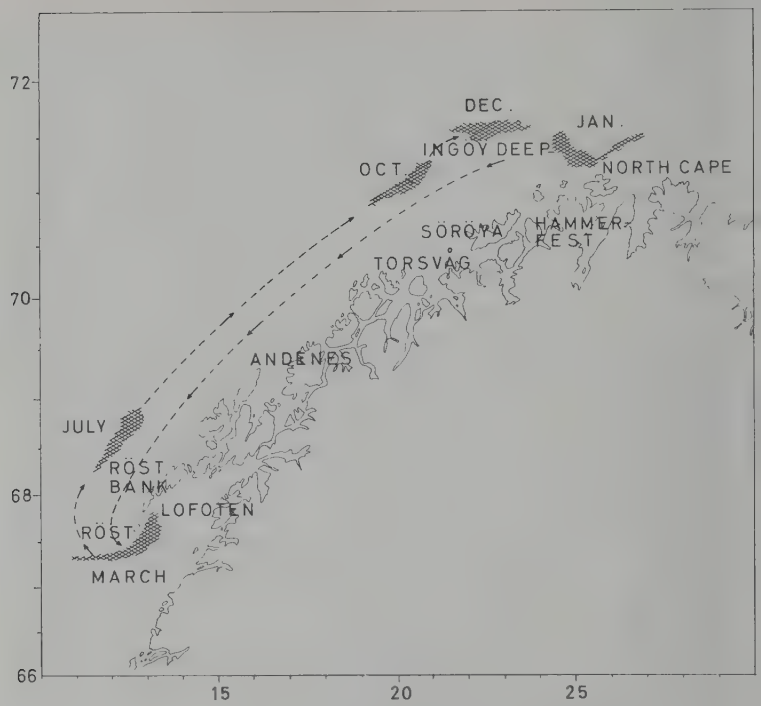

Fig. 1. The migration of the Lofoten—Røst Bank herring 1963.

broadcasted and very soon Norwegian purse seiners gathered in the area. Till March 25th about 1,5 million hl of herring were caught in the Vestfjord area, i.e. about 50 per cent of the total Norwegian winter herring catch during the season 1964.

The spent herring left the Lofoten—Røst Bank area in April. The Norwegian fishing fleet got contact with the northern component again in late August. A Soviet fleet, however, were catching herring about 200 miles northwest of Andenes during July and August. In late October the wintering area of this northern component of mature herring were located by R/V «Johan Hjort» (Devold 1964 b).

Fig. 2 shows the most likely route of the herring schools through the year 1964.

THE 1965—SITUATION

On January 17th the Norwegian research ship «G. O. Sars» located herring schools about 100 miles northwest of Torsvåg (Dragesund 1965).

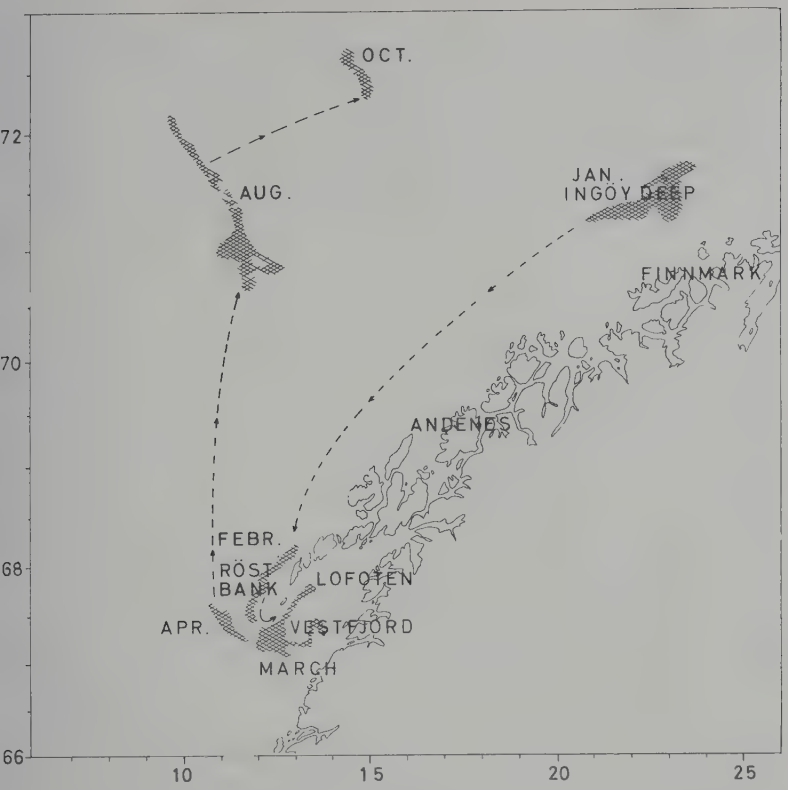

Fig. 2. The migration of the Lofoten—Røst Bank herring 1964.

The herring were found in water with temperatures between 6 and 7°C, which means that the herring had left the cold wintering area and had initiated the spawning migration.

Contact with the migrating schools was again obtained by R/V «Johan Hjort» from January 30th to February 4th along the edge of the coastal banks off Senja and Vesterålen.

Norwegian purse seiners followed the herring schools to Røst, and the spawning took place on both sides of the Vestfjord and on the Røst Bank (Devold 1965 a). The Norwegian fleet caught about 450 000 hl of herring from this northern component during the winter herring season. The Soviet fleet caught about 1,2 million hl on the Røst Bank during the same season.

In April the spent herring left the northern Norwegian coastal waters and disappeared in northwesterly direction.

The herring was again located by R/V «G. O. Sars» in the first days of August about 170 miles southwest of Bear Island. The Norwegian herring fleet was informed, and a few of the larger Norwegian purse seiners headed for the R/V «G. O. Sars» position, where they had very good fishing. There were large herring schools, which in daytime kept to a depth of between 200 and 300 m. In the afternoon the herring ascended towards the surface and during the night dispersed in the surface layer.

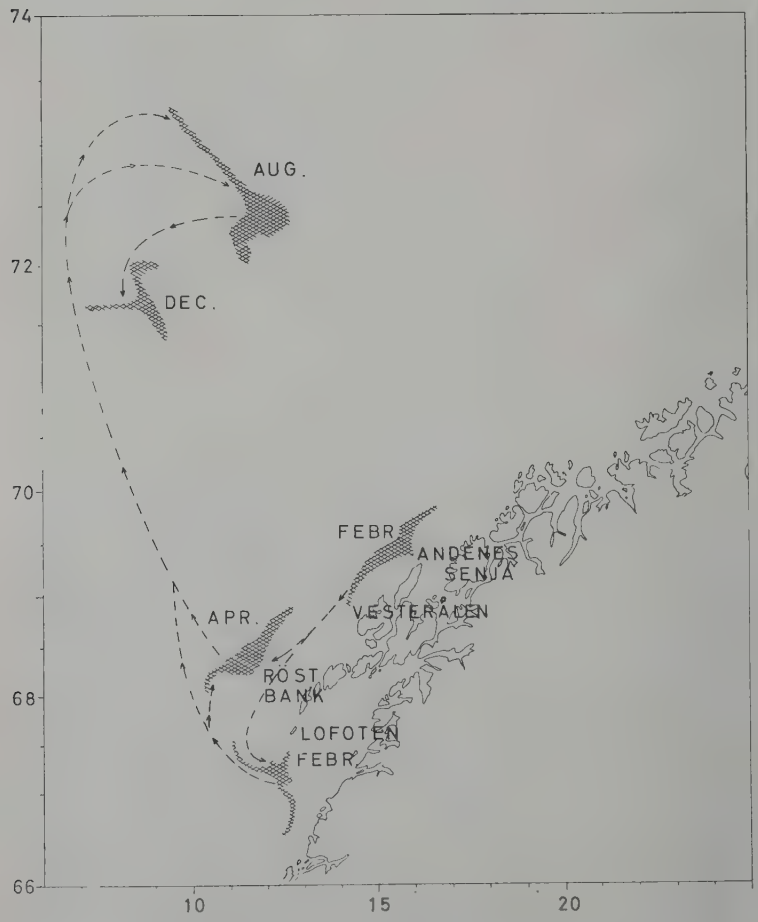

Fig. 3. The migration of the Lofoten—Røst Bank herring 1965.

The next morning schools were again formed and the herring again descended to the deeper layers (Devold 1965 b).

The wintering area where this herring spent the time between October and early January was located during a cruise with R/V «Johan Hjort» from November 24th to December 10th 1965 (Devold 1955).

Fig. 3 shows the most likely route of the Lofoten spawning herring during the year 1965.

THE 1966—SITUATION

The wintering area of the herring was visited by R/V «Johan Hjort» in early January 1966. The herring had since late November moved about 40 miles to the south, but were still keeping to water with a temperature of 3°—4°C. The schools stayed in the depths of 200—350 m day and night. On February 24th migrating schools of mature herring were located by R/V «G. O. Sars» between Andenes and Anda light house (Devold 1966).

The extremely cold winter in northern Norway in 1965—66 cooled the bankwater to a temperature lower than previously observed (Devold 1966). In February the main part of the Røst Bank was covered from surface to the bottom by water with temperatures below 3°C, and the spawning of the herring took place mainly at the western and northern edge of the bank.

After spawning the herring left the Lofoten—Røst Bank area and were again located by R/V «Johan Hjort» on June 16th in the position N 70°30' to N 71°06' and E 11°13'. The schools were moving in north-westerly direction.

Fig. 4 shows the route of R/V «Johan Hjort» in June—July 1966. The temperature in 4 m depth recorded by the sea-termograph, and the registration of herring schools are also shown.

It appears a wide area with no herring between the easterly and westerly concentrations of herring in late June and early July. The main herring component, which has the more southern distribution, has not been included in the map. It was located by the Icelandic research ships south of Jan Mayen and followed through the summer by the Icelandic herring fleet.

The movements of the herring schools are described by Jakobsson in an appendix to this paper.

Contact with the eastern concentration of herring were kept by R/V «Johan Hjort» and by a few Norwegian purse seiners from late June to July 11th. The rest of July and August the Norwegian ship

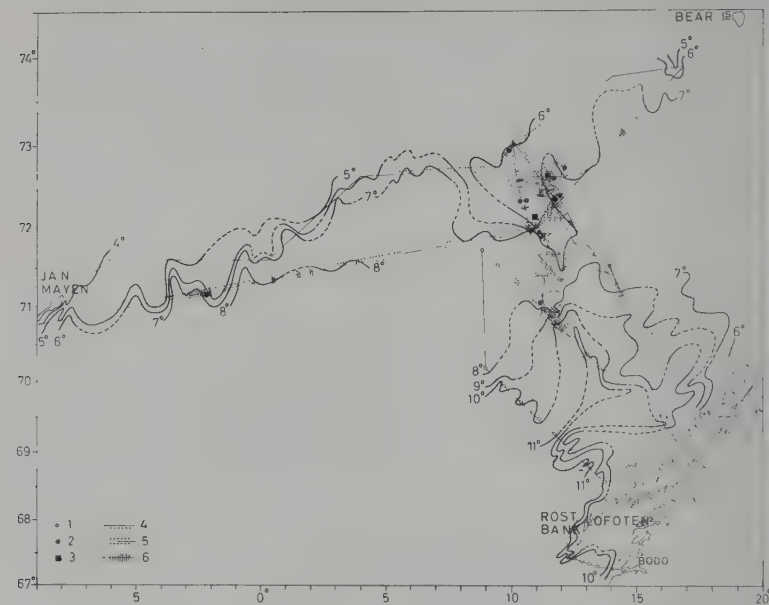

Fig. 4. Routes and stations, R/V «Johan Hjort» 1966. Temperature C° in 4 m. 1) hydrographical stations, 2) drift nets stations, 3) tagging locality. Herring concentrations: 4) very scattered, 5) scattered, 6) dense.

«Storeknut» kept contact with the herring schools. The most northerly concentrations of herring were located in the middle of August in a position about N 74°30' with a westerly limit at about E 10° (Anon. 1966). The Norwegian purse seiners were during August joined by a fleet of Soviet drift net ships. The Norwegian ships left the area in late August after fishing 400 000 hl in this locality.

Two spawning migrations to the Norwegian coastal banks during the winter herring season 1967 were expected, one coming from the north to the Røst Bank —Lofoten area and a second one from the wintering area east of Iceland to the Møre coast. On November 18th 1966 R/V «Johan Hjort» started on a cruise for locating the wintering area of the northern component of the mature herring, but no mature herring were observed. The investigations were repeated in early January and late February 1967 with negative results. In fact, there was no spawning migrations of herring to the Røst Bank—Lofoten area during the 1967 season, nor during the 1968 season. The northern component had simply disappeared.

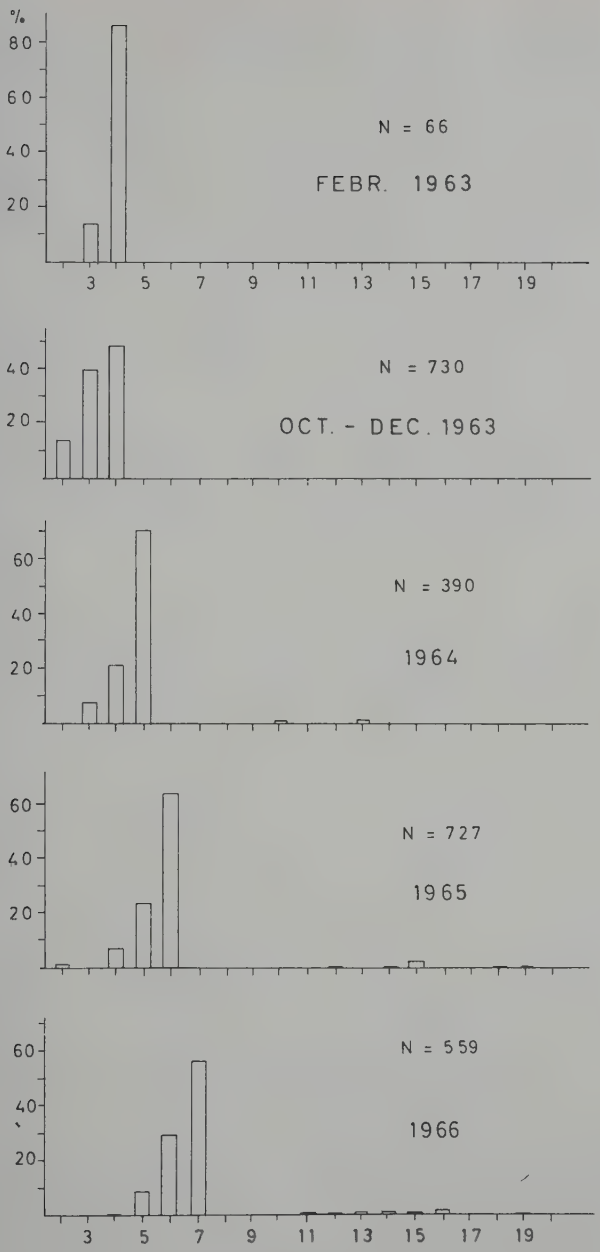

Fig. 5. Age composition off Finnmark.

THE AGE COMPOSITION OF THE LOFOTEN SPAWNING HERRING

In Fig. 5 is demonstrated the age composition in samples of herring taken in the open sea areas shown on Figs. 1—3. The samples show that the stock consists of only young herring. In February 1963 it consisted mainly of the 1959 year-class. In October—December 1963, when the herring were gathered in the Ingøy Deep, the component had received a substantial recruitment from the 1960 and the 1961 year-classes. The samples from 1964 and 1965 show the same picture, but the herring are one and two years older respectively.

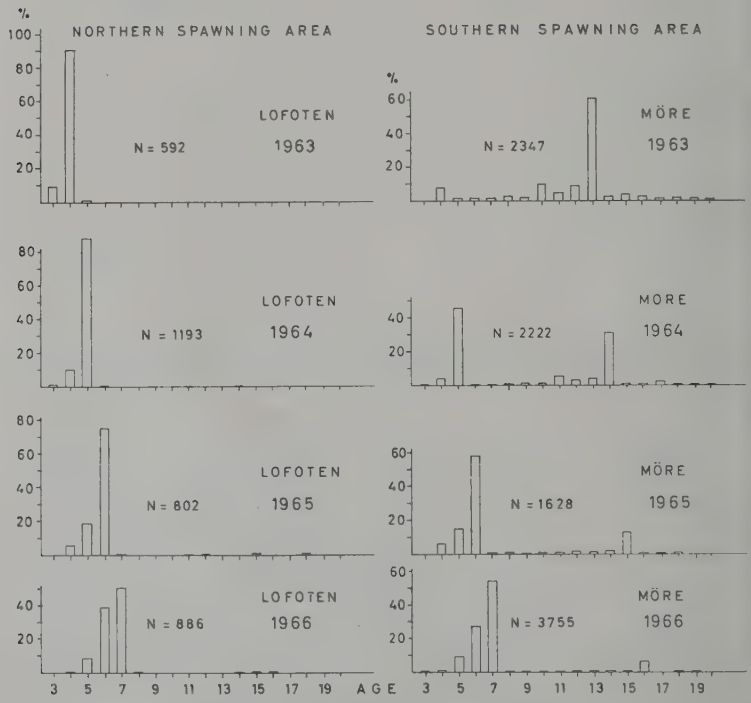

Fig. 6. Age composition Lofoten—Møre.

Fig. 6 shows the age composition of the Lofoten—Røst Bank spawning herring and the age composition of the herring which have followed the southern spawning migration route from the wintering area east of Iceland. In 1963 the southern component mainly consisted of old herring with the 1950 year-class dominating. The herring spawning in Lofoten

showed the same age composition as the herring caught off Finnmark in late February. The herring which arrived in Lofoten on March 20th 1963 is therefore supposed to have migrated from North Cape to the Lofoten spawning area.

In 1964 a fairly great proportion of the 1959 year-class had joined the herring in the wintering area east of Iceland. They followed the southern spawning migration route and spawed together with the older herring in the Møre area.

In the Lofoten—Røst Bank area the spawning herring consisted only of young herring belonging to the 1959 and 1960 year-classes and a few to the 1961 year-class. The spawning herring showed the same age distribution as did the herring wintering in the Ingøy Deep.

During the winter herring seasons of 1965 and 1966 the age composition of the herring spawning off Møre, shows that the old herring were still important, and that the spawning stock in the Lofoten area contained only younger year-classes with the same age distribution as the samples collected in the Bear Island area during the corresponding summers.

THE SPAWNING—CLASSES

The individuals within a stock which have attained maturity in the same calendar year constitute a spawning-class (Rollefsen 1933).

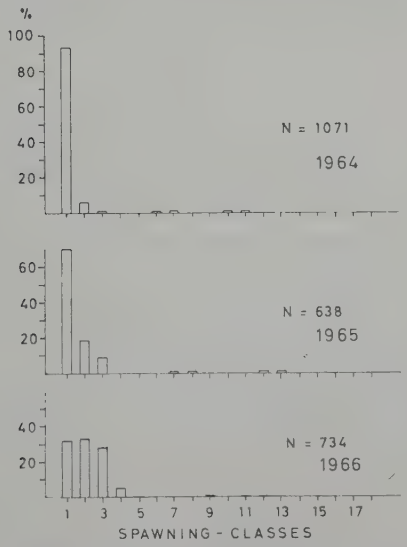

Fig. 7. Spawning-classes of the Lofoten—Røst Bank herring.

The herring which were found in the Røst area in March 1963 were first time spawners mixed with about 20 % of immature herring. Fig. 7 shows the spawning-classes of the herring during the spawning season in the Lofoten area during 1964—66. In 1964 the spawning stock of herring was composed of first time spawners and second time spawners. When the herring were spawning in the Lofoten—Røst Bank area in 1965, the third year in succession, the stock consisted of first, second and third time spawners. The following year, in 1966, there were first, second, third and fourth time spawners.

CONCLUSIONS

The conclusions we can draw so far are:

1. During the years 1963—66 a separate stock unit of the Atlanto—Scandian Herring occurred off northern Norway. It consisted of herring belonging to the year-classes 1959, 1960 and 1961.
2. The stock had a spawning, feeding and wintering area, separated far from the main stock of mature Norwegian herring.
3. In the autumn 1966 the whole stock disappeared from the area.
4. During the winter herring season in 1967 and 1968 there were no spawning migration of herring to the areas off northern Norway.
5. The vertical movements of the herring schools in the wintering area are connected with the light. There are no vertical migrations of the schools in areas where it is dark day and night.

SUMMARY

1. On February 2nd 1963 mature herring belonging to the Atlanto—Scandian herring were located off Finnmark between North Cape and Sørøy.
2. The herring arrived in the Røst Bank—Lofoten area, where it was recorded spawning late March 1963.
3. The migrations of the herring were seasonally followed by Norwegian research ships and hired ships through the years 1963—1966. The most likely migrations are demonstrated in Figs. 1—3.
4. The herring were recruited from the main stock of immature herring and consisted of the year-classes 1959, 1960 and 1961.
5. In 1963 only first time spawning herring occurred. In 1964 there were first and second time spawners. In 1965 there were also third time spawners and during the spawning season in 1966 there were first, second, third and fourth time spawners.

6. The herring had their own spawning, feeding and wintering areas separated far from the main stock of Norwegian winter herring.
7. In the autumn 1966 the stock unit disappeared. During the winter season 1967 and 1968 there was no spawning migration to the Lofoten—Røst Bank area.

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APPENDIX

HERRING MIGRATIONS EAST OF ICELAND DURING THE SUMMER AND AUTUMN 1966 AND 1967

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SURVEY RESULTS

The first contact with the feeding summer migration of the Norwegian herring was in 1966 made on May 8th when herring was located in a large area between N 64° and N 65° and from W 6° and W 8°. The herring were concentrated in large migrating shoals and obviously well suited for purse seining. The Icelandic herring fleet was informed, and the first catches were taken on May 12th. The major part of this migration quickly moved north of N 66°, and by the end of June and the beginning of July the migration had assembled in the region south and southeast of Jan Mayen. It is quite certain that the major part of this herring migration remained in the Jan Mayen area throughout July although some part may have migrated further NE, all the way to the Bear Island area. At the beginning of August there was a distinct tendency for a westward movement of the herring in the Jan Mayen area, and by August 10th the westernmost part of the herring shoals had migrated as far west as W 14° between N 69°30' and N 70° where they met the eastern boundaries of the cold waters west and southwest of Jan Mayen. Thus the temperature in the surface layers where the shoals assembled, was about 4,5°—5,5°C, but a few miles further west the sea temperature was about two degrees lower.

During the latter half of August the herring migrated very fast in a south and southeasterly direction. During this phase of the migration the main concentration followed the eastern border of the cold East Icelandic current and approached the east coast of Iceland when it had reached the southern limit of the current. This appeared to be between N 64°30' and N 65°. Thus the herring covered 5° latitudes or about 300 n.m. during the last 10 days in August.

As discussed by Devold (above), another part of the Norwegian herring stock had during the previous years not entered Icelandic waters, but stayed in the Bear Island region during summer and winter and spawned in the Lofoten area. Judging by the change of positions

of the Russian drifter fleet in early September 1966 there were clear indications that this stock unit had started a westerly migration towards Jan Mayen. This continued throughout September. In early October the herring concentrations were located in an area between N 60° and N 70° from W 9° to W 8°. Thus dense concentrations were observed in an area stretching some 60 n.m. from north to south and some 20—25 n.m. from east to west. Judging from the sonar surveys the concentrations were certainly of no less magnitude than the previous August—September migration. During the period from October 15th to October 25th the herring moved very quickly SSE and followed a similar route as the previous migration in August. The only difference was that in October the herring did not go as far west between N 69° and N 70° as the August migration. During November and December both migrations remained in the traditional overwintering area some 60—120 n.m. off the southern coast of East Iceland. There is therefore reason to believe that during the overwintering period shoals and individuals of both stock units had intermixed considerably prior to the spawning migration which commenced in January 1967.

The first herring concentrations were in 1967 located on May 9th in a wide area from N 65°—N 67°30' between 0° and W 3°. There was obviously a large quantity of herring in this area concentrated in dense migrating shoals. As compared with the previous year the herring were in 1967 much further east (difference of 4—7° longitudes) and north (1—2° latitudes) than at the same time in 1966.

The herring moved north and northwest during the second half of May. By June 10th the main concentrations had reached N 70° and were between W 02°30' and W 05°30'. At this stage a very curious thing took place: A considerable proportion of the herring concentrations turned west and southwest. By June 20th this part of the stock had reached N 68°45' and as far west as W 8°45'. This indicated that the summer distribution of the herring might be somewhat similar to the distribution the previous year when one «half» of the stock spent the middle of the summer south and southeast of Jan Mayen whereas the other «half» stayed some 300 n.m. northwest of northern Norway. However, the herring quickly turned after entering the very cold water in the areas south of Jan Mayen and retraced their path northeast. By the beginning of July the herring were 80 n.m. east of Jan Mayen. Later they followed the northeasterly course already taken by the other «half» of the stock and spent the summer in the Spitzbergen--Bear Island region as discussed elsewhere in this paper. Norwegian herring did not enter the western part of the Norwegian Sea, i.e. west of the 0 meridian, in any significant quantity until late September when the herring took

the traditional route towards the overwintering area off the coast of East Iceland. In 1967 the route taken by this migration was almost identical to the one taken by the 2nd herring migration in October 1966 as discussed above. However, both in 1966 and 1967 some herring did not take the northerly routes during the summer as described above, but remained off the East coast. In 1966 there was a considerable quantity in this area throughout the summer. During July 1966 the herring were scattered and difficult to distinguish because large quantities of *Gadus poutassou* were present in the area. At the beginning of August the herring assembled in good shoals suitable for purse seining and in sufficient quantity to support good fishing for 2—3 weeks.

Similarly, in 1967 Norwegian and Faroese drifters caught some herring off the east coast of Iceland in August but the catches were small and the herring never formed proper shoals for purse seining. The quantity in 1967 in this area was much less than in the previous year. It should also be noted that in 1966 the summer herring caught off the East coast consisted of many year-classes where the one from 1959 dominated. However, judging by a sample from a Faroese drifter the dominant yearclass off the East coast in 1967 was that from 1950, i.e. 17 year old herring.

TAGGING RESULTS

The joint Icelandic—Norwegian herring tagging experiments which started in 1948 have supplied a great deal of information. It is sufficient to mention the long range migrations between the spawning grounds off western Norway and the feeding grounds off Iceland. These migrations were postulated by Fridriksson (1944), and has been proved by tagging experimets. The rate of return from the experiments carried out on the feeding grounds off Iceland have been so consistent during the Norwegian winter fishery that it has proved possible to conduct stock strength studies on the basis of the rate of tagging returns.

Although the results of the Icelandic Norwegian herring tagging experiments have thus shown for the last twenty years that the Norwegian herring migrates between the spawning grounds of western Norway and the summer feeding grounds off Iceland, the evidence that herring migrated directly from the Barents Sea to the Icelandic north coast is much more recent. The first time such a migration was shown by the results of these tagging experiments was in 1962. In late August and early September great concentrations of immature three year old herring were located some 60—80 n.m. off the North coast of Iceland between

W 16° and W 18°. During the subsequent fishing there, 4 tags were recaptured from a tagging experiment carried out in the autumn 1961 off northern Norway. Since these herring were immature, there could be no doubt that they had migrated directly from northern Norway before recruiting to the spawning stock off western Norway. Similar returns from «Feitsild» tagging experiments were also received during the period 1963—1965. Thus there can be little doubt that immature herring off northern Norway have migrated more or less regularly to the Icelandic area and have to some degree directly contributed to the overwintering herring concentrations off East Iceland.

Now that this migration route has been established not only from evidence of earlier sonar surveys (Devold 1952), but also from tagging of «Feitsild», let us consider the tagging returns in 1966 i.e. the year when according to the sonar surveys a whole stock unit of mature herring migrated from the Bear Island region to the overwintering grounds off East Iceland. On June 20th 1600 herring were tagged by the Icelandic herring search boat «Hafthor» in position N 69°50' and W 7°10', i.e. south of Jan Mayen. During the following months 31 tags were returned from herring caught in that area and in the area east of Iceland. Three tags were recovered from herring landed in Norway during the Norwegian herring fishery in the Bear Island region in July—August 1966. These returns suggest that part of the western component probably had migrated eastwards and joined the herring in the Bear Island region during the summer 1966.

In 1966 it was shown by means of sonar surveys that a whole stock unit of mature herring migrated from the Bear Island region to the overwintering grounds off East Iceland. As regards this westward migration it is fortunate that the Norwegian R/V «Johan Hjort» on July 5th 1966 tagged 1 500 herring in the Bear Island area. One of theese was recaptured in the Bear Island area in August the same reason. Two were recaptured off East Iceland in October 1966, three in November and 12 in December. A total of 17 tags were thus returned from the overwintering fishery off East Iceland. Direct migrations of mature herring between these distant areas were thereby established in 1966. For comparison it should be mentioned that during the same period 37 tags were returned from the winter herring tagging experiment carried out during the Norwegian fishery off western Norway 1966. A total of 3 300 herring were tagged. Thus the rate of returns from these two experiments were very similar. It should, however, be noted that during the summer season proper, i.e. prior to October, no tags from the Bear Island region were returned while returns were received from the winter herring tagging experiments.

Fig. I. Tagging and recapture localities and migrations of herring till March 1967. 1) Icelandic tagging locality, 2) Norwegian tagging locality, 3) recaptures.

During January—March 1967 six tags from the Bear Island tagging were returned from the Faroe Banks spawning area and 52 from the spawning area off Møre.

In 1967 the rate of returns during the feeding and overwintering season was much higher from the Bear Island tagging experiment, i.e. 39 tags as compared with 33 tags from the winter herring tagging experiment (Fig. I).

A further evidence of the 1966 migration of the Bear Island—Lofoten stock unit to the overwintering grounds off East Iceland can be derived from a tagging experiment of 700 herring on the Lofoten spawning grounds on February 27th 1965. In spite of the great quantity reduced at the Icelandic reduction plants (approx. 0,5 mill. tons) no returns were received from this experiment during the 1965 summer and autumn season. In 1966 there were on the other hand 12 returns from this experiment.

Thus the tagging results all support the results of the sonar surveys to the effect that the stock unit which had developed in the Bear Island—Lofoten region during the period 1963—1966 undertook in the autumn of 1966 a massive 600—800 n.m. migration to the overwintering grounds east of Iceland where the herring mixed with the other part of the Norwegian stock previously assembled in this area. During the subsequent spawning as well as throughout the feeding and overwintering periods in 1967 these herring behaved as a single population unit.

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ZOOPLANKTON AND THE DISCONTINUITY LAYER IN RELATION TO ECHO TRACES IN THE OSLOFJORD

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INTRODUCTION

During cruises with R/V «Gunnar Knudsen» it was discovered that the echosounder nearly always recorded echoes from the depth of the thermocline. In accordance with the appearance of the traces (cf. Fig. 2) the term *echo-bands* was introduced.

The echo-bands might be caused by reflection from the border layer between two water masses (Hashimoto and Maniwa 1956, Banse 1957, Lenz 1965) or from accumulated particles in this layer

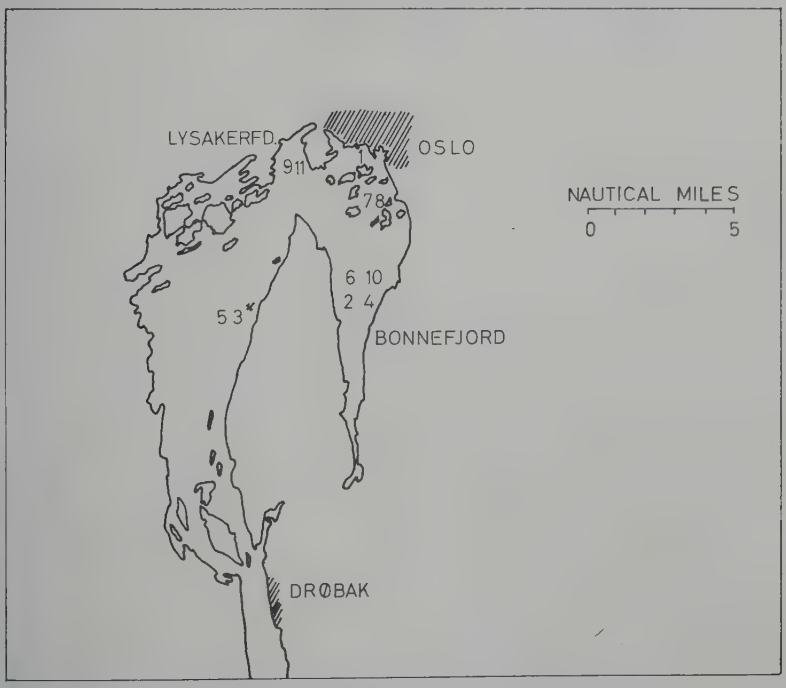

Fig. 1. The Oslofjord and observation stations.

(Trout, Lee, Richardson and Harden Jones 1952, Cushing, Lee and Richardson 1956, Weston 1958, Olsen 1960). The particles again might be living plankton concentrating in the layer or dead organisms and particles retarded in their sinking.

From June 1963 through April 1964 attempts were made to reveal the possible sources for the observed echo-bands in the Oslofjord (Fig. 1).

METHODS

The SIMRAD echosounder used in the present investigation had a frequency of 38.5 Kc/sec. and two optional puls lengths, which were 1 and 0.1 millisecond respectively. In order to obtain distinct recordings the shortest puls length was always applied. If applying the longer puls length two narrow echo-bands might coalesce and make one broad band. The speed of the wet echosounder paper was 1.3 cm per minute. The transmitted sound impuls was constant, the source level measured as sound intensity 1 m from the transducer being 105 dB// 1 μ bar, but the the received signals could be amplified. The amplifier had 11 positions and the corresponding amplifications are given in Table 1. The lowest echo that could be recorded was — 40 dB// 1 μ bar.

Table 1. Positions of the amplifier, the corresponding amplification of a received impuls and minimum recordable signal (MRS) in dB//1 μ bar.

Position	0	1	2	3	4	5	6	7	8	9	10
Amplification:	?	?	1000	4000	7500	10000	15000	30000	45000	80000	80000
M R S:			—21	—27	—30	—31	—33	—36	—38	—40	—40

To find a measure of the strength of a received echo, the amplifier was turned successively down until the echo disappeared (Fig. 2) and the last position before its disappearance was used as a measure. It was not possible to distinguish echoes above 4 m since the transmitter was submerged underneath the hull 1.3 m and the receiver had a further 2—3 m blockaded area.

The reflection factors in Table 3 are calculated from the formula:

$$\frac{I_r}{I_i} = \frac{((\varrho c)_2 - (\varrho c)_1)^2}{((\varrho c)_2 + (\varrho c)_1)^2}$$ (Horton 1957).

I_r is the acoustic intensity of the reflected wave and I_i the acoustic intensity of the incident wave, $(\varrho c)_1$ is the specific acoustic impedance in the medium on the side containing the sound source and $(\varrho c)_2$ the specific

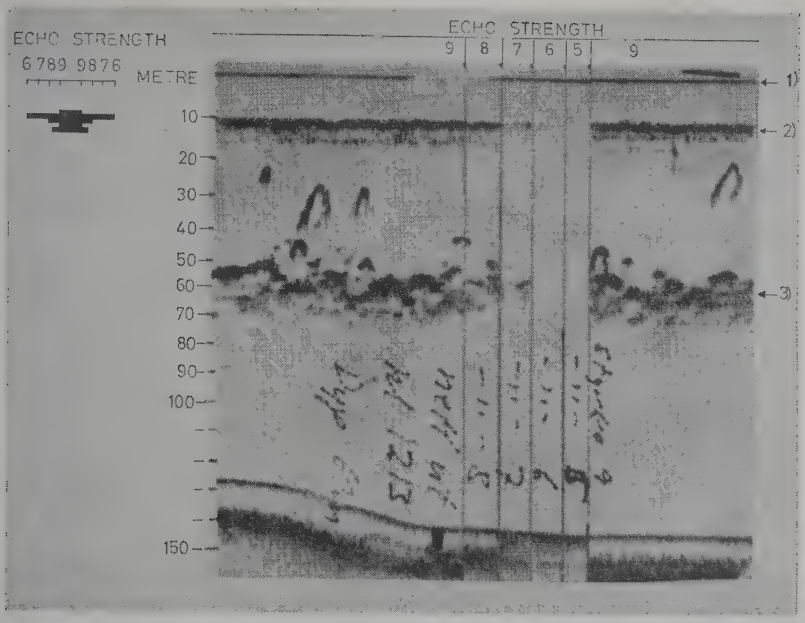

Fig. 2. Example of echo-bands reproduced in Fig. 4. 1) transmitter depth, 2) echo-band, 3) supposed herring and(or) sprat recordings.

acoustic impedance on the other side of the boundary plane. ϱ is the density and c the sound velocity in the respective media. The formula is based on the assumption that normal incident sound waves are reflected from an ideal plane surface separating two ideal fluid media which are incapable of exerting shear stresses. The acoustic pressure of the wave in the second medium must equal the acoustic pressure of the wave in the first medium, both pressures being taken immediately adjacent to the boundary plane. The component of volume velocity normal to the plane with which fluid from one side approaches it, must for an infinitesimally short distance equal the component of volume velocity normal to the plane with which fluid on the other side moves away.

The sound velocities are calculated from the formula given by Midttun (1964):

$$v_{t,s,p} = 1400 + 4.9\ t - 0.044\ t^2 + (1.32 - \frac{t}{100})\ S + 0.018\ (1 - \frac{t}{100})\ p$$

$v_{t,s,p}$ is the sound velocity in m/sec. at the temperature t° C, salinity S $^0/_{00}$ and the pressure p in decibar (or metre).

Plankton samples were taken by means of a horizontally towed net. The net had a square opening 1 m by 1 m with the mesh size 1 mm by 1 mm. There was no wire in front of the opening, and the net was kept down by means of a canvas depressor. Towing time was half an hour from the net had reached the wanted depth till heaving was started. The speed of the vessel was 1.5—2.0 knots, implying that the net was towed 1300 to 1800 m in the proper depth. The percentage of plankton caught during lowering and heaving the net was assumed to be very low compared with plankton caught in the proper depth. The towing depth was determined from measuring the length and the angle of the wire. Attempts were made to sample from the strongest echo-band or the strongest part of it. The net was also towed under and over these layers.

Smaller plankton animals were collected with a two inch rotary pump (capacity 100 l/min.) equipped with an armed two inch rubber intake hose. 300 litres of water were filtered trough a fine mesh plankton net (125 μ).

The samples were preserved on bord in 4% formaldehyde in water, and the organisms were counted in the laboratory, as a rule in subsamples of one or two tenths of the entire sample. Subsamples were obtained by means of the plankton divider described by Wiborg (1951).

The bathythermograms were adjusted to the thermometer readings from the Nansen water bottles. Some samples for salinity determinations were taken from the water bottles, but the majority of the salinity determinations were made on water obtained through the pump. The intake of the hose was mounted between two horizontal circular plates with a diameter of 42 cm and a distance between the plates of 8 cm in order to as far as possible get the water from the measured depth. Comparable samples taken with water bottles and the plankton pump gave a difference in salinity corresponding to about 1 m difference in sampling depth, the water bottle always sampling above the pump. Banse (1955) similarly found a difference of 1.5 m. It was assumed that the figures here obtained from the pump were correct, and these figures were therefore applied when available.

RESULTS

Several observations during night cruises showed that artificial light did not affect the echo-bands implying that reflections were not caused by phototactic organisms, the fact that the echo-bands were found in the same depth both day and night indicated the same. In some cases

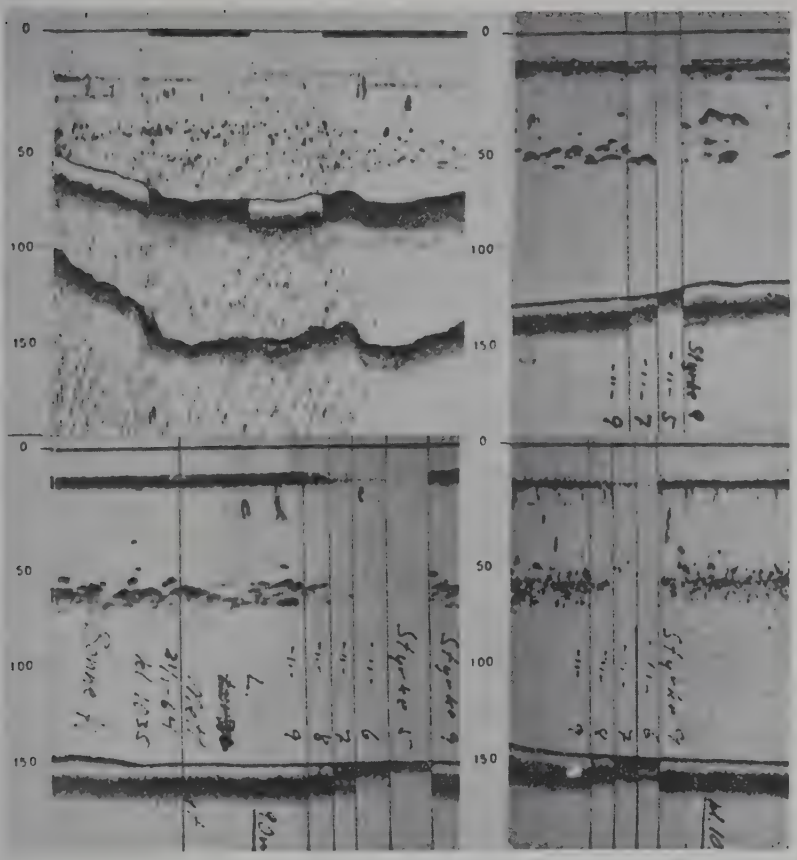

Fig. 3. Different types of echo-bands observed.

only one single echo-band was recorded, in other cases there were several ones, up to five, one just underneath the other (Fig. 3).

The results from the tow net are given in Table 2. All these samples were taken during daylight. The greatest displacement volume of plankton was found below the echo-bands at all the four stations. Correspondingly the numbers of organisms were highest below the layer except at Søndre Steilesand where a great number of fish eggs occurred. Fish eggs, when present, had always the maximum in the scattering layer, *Pleurobrachia pileus* (O. F. Müller) also showed maximum abundance there at the stations 3 and 4, but had a different distribution pattern at the stations 1 and 2 (Table 2). The big jellyfishes *Cyanea capillata* (L.) and

Table 2. Plankton animals caught with the horizontally towed plankton net. Numbers and displacement volumes of the samples above, in, and below the scattering layer.

Station 1. Vippetangen, 26. June 1963, 1130—1700 hours. Echo-bands at 10 and 12 m, strength 7. Depth in m	5	9.5	14
Rathkea octopunctata	0	0	1 854
Lensia conoidea	0	6	481
Aurelia aurita	4	6	2
Pleurobrachia pileus	1	9	72
Other organisms	3	10	267
Total	8	31	2 676
Displacement volume ml.[1])	1	1	18

Station 2. Bonnefjorden, 1. July. 1963, 1200—1600 hours. Echo-band at 11 m, strength 9. Depth in m	3.5	10	20
Rathkea octopunctata	0	0	2 180
Eutonina indicans	0	66	10
Lensia conoidea	5	74	6 340
Aurelia aurita	6	15	0
Cyanea capillata	0	10	0
Pleurobrachia pileus	3	61	many[2])
Fish eggs	5	18	10
Other organisms	29	46	150
Total	43	272	8 680
Displacement volume ml.[1])	1	43	100

Station 3. Søndre Steilesand 2. and 3. July 1963, 1000—1500 hours. Two to four echo-bands at 8—16 m, strength 9—5. Depth in m	4	11	18
Eutonina indicans	0	1	73
Lensia conoidea	0	1	3
Aurelia aurita	2	1	0
Cyanea capillata	1	4	6
Pleurobrachia pileus	0	36	25
Fish eggs	3	316	179
Other organisms	11	70	104
Total	15	393	365
Displacement volume ml.[1])	1	4	64

cont.

Table 2 cont.

Station 4. Bonnefjorden, 21. Jan. 1964, 1000—1400 hours. One echo-band at 8—14 m, maximum strength 5 at 11 m. Mesh size in this case 10 mm.

Depth in m	5	10	35
Lensia conoidea	0	17	236
Pleurobrachia pileus	0	23	1
Sagitta elegans	0	0	4
Other organisms	0	3	11
Total	0	43	252
Displacement volume ml.[1])	0	2	14

[1]) In the displacement volume *A. aurita* and *C. capillata* are not included.

[2]) A great number of *P. pileus* disintegrated because of unsuited formalin concentration.

Aurelia aurita (L.) also sometimes occurred in greater numbers in the echo-band layer. Large jellyfishes may give echo-traces, but not with the appearance of an echo-band (Beyer, verbal information). The greatest concentrations of the other species were as a rule found below the level of the echo-band. Macroplankters thus seem not to present a probable source of sound scattering in the present cases.

Fig. 4 shows the distribution of smaller plankton animals taken with the pump. It appears that the observed maxima correspond fairly well with the echo-bands at the stations 6, 7 and 10. The total number of smaller plankton at the other stations have either no distinct maxima or the maxima are not in the depths of the echo-bands.

Regarding the single species, the larvae of the polychaet *Polydora ciliata* (Johnston) had a very distinct maximum in the scattering layers both at St. 6 and 7, but at St. 8, taken at night, the maximum was clearly above the layer. Some other species had their maxima in the scattering layer, but never in such amounts that they could explain the echo-bands.

If we compare the echo-bands with the corresponding hydrographic condition, the echo-bands were in most cases found at depths where great gradients in salinity and(or) temperature occurred (Fig. 4).

There is no good correlation between the theoretic calculated echoes and the strengths at which they are recorded (Table 3), but the two lowest calculated echoes had corresponding echo-bands which only were recorded at strength 10 and 9.

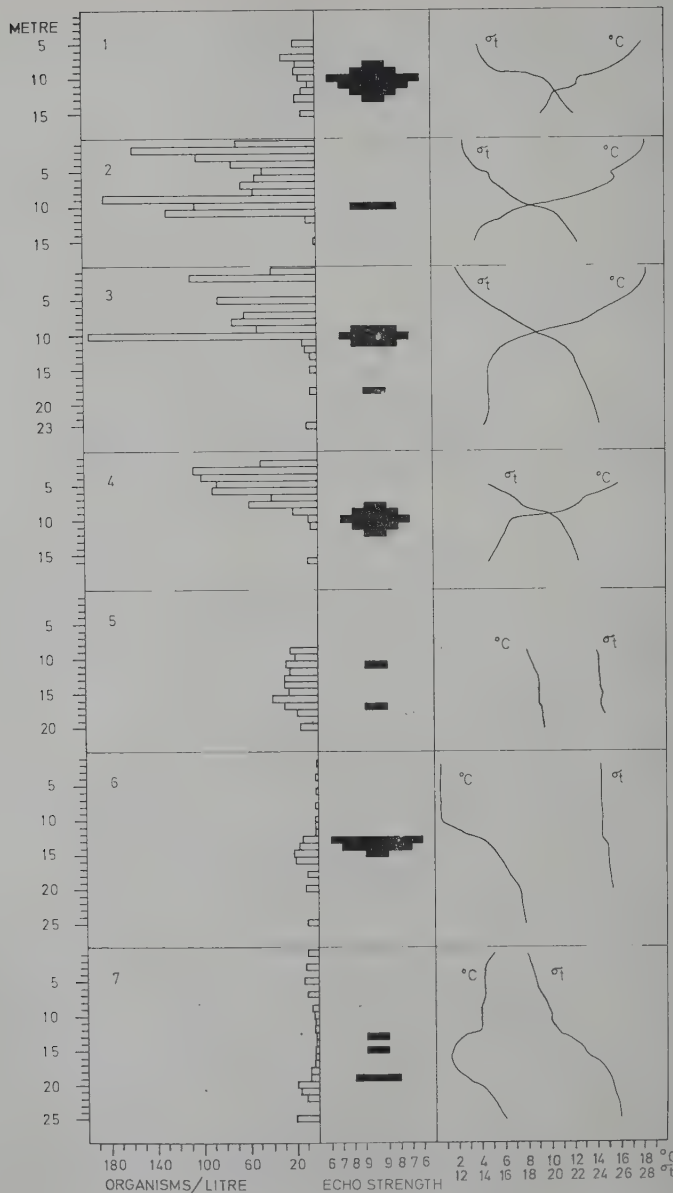
METRE
1
2
3
4
5
6
7
σt
°C
180 140 100 60 20
ORGANISMS/LITRE
6 7 8 9 9 8 7 6
ECHO STRENGTH
2 4 6 8 10 12 14 16 18 °C
12 14 16 18 20 22 24 26 28 σt

Table 3. Strength and properties of echoes from the scattering layers where water was sampled with one metre depth intervals. The calculations are made from two successive observations in the layer where the largest difference was recorded.

St	Date	Echo strength	Depth	t_2—t_1	σt_2— σt_1	$(\varrho c)_2$— $(\varrho c)_1$	Geometric spreading loss dB	Reflection factor dB	Theoretic echo received. dB// 1 μ bar
5	13 08 63	6	8—12	—2.00	2.88	1.17	36	—67	2
6	14 08 63	8	10	—3.00	1.71	—7.09	36	—52	17
7	15 08 63	7	9—11	—2.25	0.95	—5.51	36	—55	14
8	16 08 63	7	8—12	—4.25	1.08	—14.37	36	—47	22
9	05 12 63	9	10	0.25	0.32	2.10	36	—63	6
9		9	17—18	0.00	0.20	0.64	48	—74	—17
10	28 01 64	6	13—15	1.50	0.39	8.18	43	—51	11
11	22 04 64	9	13	—1.75	1.08	—4.56	41	—57	7
11		9	15	—0.25	0.40	0.18	45	—84	—24
11		8	19	0.75	0.27	4.23	49	—57	— 1

DISCUSSION AND CONCLUSION

If only the geometric spreading of the sound wave is considered as transmission loss, the theoretical calculated echoes should lie between 22 and — 24 dB// 1 μ bar, implying that all calculated echoes have higher intensity than minimum recordable signal for the present echo sounder, — 40 dB// 1 μ bar. In fact most of the echo-bands should have been recorded with far less amplification than they were. However, the ideal conditions required to give correct results with the formula for reflection factors are surely not fullfilled. The calculations are made from observations taken with one metre interval, and the difference between the two observations are considered to take place somewhere within this metre without having any vertical dimention. The vertical distributions of some echo-bands show that this is not the case, the sound must have been reflected from more than one plane. Hence the reflected sound waves are surely of lower intensity than calculated. However,

←

Fig. 4. Total number of plankton taken in the pump and the corresponding echo-bands, temperature and density. 1) station 5, Aug. 13, 1963, 1130—1600 hours, 2) station 6, Aug. 14, 1963, 1000—1500 hours, 3) station 7, Aug. 15, 1963, 1000—1600 hours, 4) station 8, Aug. 16—17, 1963, 2100—0030 hours (dark), 5) station 9, Dec. 5, 1963, 1330—1600 hours, 6) station 10, Jan. 28, 1964, 1000—1500 hours, 7) station 11, Apr. 22, 1964, 1030—1600 hours.

there is room for relative great reductions till the minimum recordable signal for the SIMRAD echosounder is reached. More exact conclusions will require both better acoustical equipment and more accurate hydrographical measurements.

The echograms are affected by both the situation in the sea and the electronics of the echosounder. It is, therefore, difficult to compare results obtained from different echosounders. Barry, Barraclough and Herlinveaux (1962)got different recordings of the same scattering layer with a 12 Kc/sec. and a 30 Kc/sec. echosounder.

Northcote (1964) recorded 9—12 mm long Chaobourus (gnat) larvae when using a 200 Kc/sec. echosounder.

From the present investigation it is concluded that zooplankton is not responsible for the echobands, similar to what Lenz (1965) found using a 30 Kc/sec. echosounder. The strong echobands recorded during the winter, when the water was clear and contained comparatively little phytoplankton and detritus also support Lenz's findings that the phytoplankton and detritus do not cause echo-bands. The material indicates, however, that the physical border between two water masses might be the real cause of the echo-bands in the Oslofjord.

SUMMARY

1. Using high amplification on the 38.5 Kc/sec. echosounder echoes from the depth of the discontinuity layer in the inner Oslofjord were mostly observable.
2. The distribution of zooplankton was analysed from samples taken with a plankton pump and tow nets.
3. The vertical distribution of zooplankton, biomass, total number and number of the different species demostrated that such organisms were not responsible for the echoes.
4. Calculations made from hydrographic data are the bases for assuming that these special echo traces are caused by the border layer between two water masses.

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THE AUTUMN SPAWNING GROUP OF HERRING IN THE NORTHEASTERN NORTH SEA

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INTRODUCTION

The Norwegian herring fishery in the North Sea started in 1898 (Iversen 1904). During the first half of this century the effort was low, particularly due to good profitability in other herring fisheries; i.e. those based upon the Norwegian spring spawning stock. The decline in the catches of the Norwegian winter herring fishery in the end of the fifties, however, induced the fishermen to a heavier exploitation of the herring stocks in the North Sea. The landings from the North Sea, which before the end of the fifties were below 100 000 hl, rose to nearly 200 000 hl in

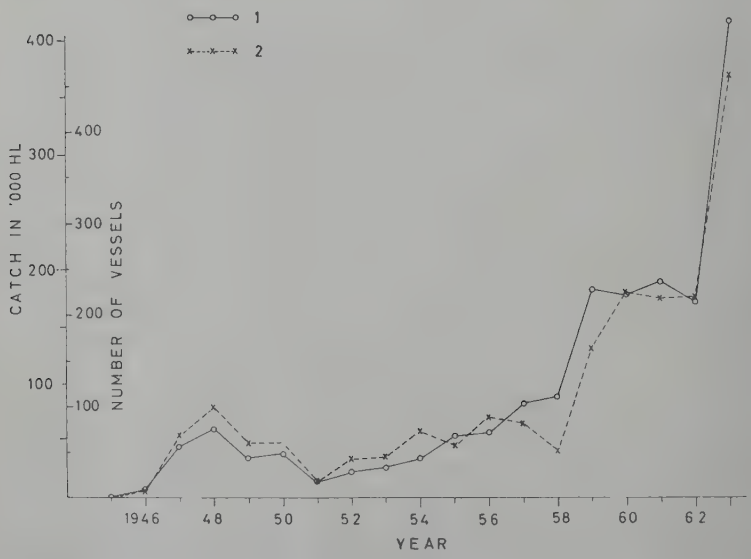

Fig. 1. Total catch of herring from the North Sea and Skagerrak and number of vessels participating in the fishery, 1945—1963. 1) total catch, 2) number of vessels.

the years 1959—62 and in 1963 to more than 400 000 hl. The total catches and number of vessels participating in this fishery during the period 1945—63 are shown in Fig. 1.

The official statistics of the effort in the herring fishery include all vessels with catches to a value of more than 5000.—N. Kr.

The majority of these vessels were mainly fishing for other species than herring, particularly Norway Pout and shrimps. The herring fleet in the early sixties consisted only of approximately 60—70 vessels.

The main gear used in the herring fishery was bottom trawl and from 1959 onwards also pelagic pair trawl. A few drifters have occasionally participated in this fishery, and during autumn 1963 some catches were also made by purse seiners.

At the beginning of this century the major part of the catches was made during summer in the area east of Shetland and during autumn on the Viking Bank. From the end of the fifties the fishery has been concentrated to the northeastern North Sea and the western entrance of the Skagerrak, particularly along the western slope of the Norwegian Channel. Except for the months June—July, when the trawlers switched over to fish Sand Eel, the herring fishery went on throughtout the year. The distribution of the main areas of fishing in 1962 are summarized in Fig. 2. The landings from the various areas have been grouped into two-monthly periods. From this figure a regular pattern of movement emerges. In January—February the majority of the catches came from the area west of Utsira.

During March—April good catches were taken further north, between Utsira and Bergen about 20—40 nautical miles off the coast.

In July—August the main area of capture shifted to southwest and more seaward, especially to the West Bank area. A productive fishing continued on this fishing ground in September and October, while good catches were also taken on the Fladen Ground.

In November—Desember the main centre of activity was in the Egersund Bank—Coral Bank area.

The northeastern North Sea is supposed to be a mixing area of various populations of spring and autumn spawned herring. The spring spawning group of herring, which in recent years contribute a minor part of the herring stocks in this area, have been investigated earlier (Haraldsvik 1968). The autumn spawned herring in the north-eastern North Sea is supposed to originate from:

1) The «Bank» herring stock (Buchan and Dogger spawners). Spawning grounds from Shetland in the north to the Dogger Bank in the south. Spawning time from August to October.

Fig. 2. Distribution of the Norwegian North Sea herring catches (two-monthly periods) in 1962. 1) Jan.—Febr., 2) March –April, 3) May—June, 4) July—Aug., 5) Sept.—Oct., 6) Nov.—Dec., 7) frequency scale in 1 000 hl.

2) The «Downs» herring stock, Spawning grounds in the southern North Sea and eastern English Channel. Spawning time in November and December.
3) The northern Kattegat herring stock (Koppergrund). Spawning grounds in the northeastern Kattegat. Spawning time in September and October.

The non spawning distribution of these stocks are to some extent known from investigations on meristic characters and tagging experi-

ments. A review of the migration pattern of these stock is given by Parrish and Saville (1965).

The differences in meristic characters between spawning populations may be a results of differences in genotype, or of differences in environmental factors operating on one genotype, or of both these effects acting together. The plasticity in meristic characters presents the greatest difficulties in distinguishing the individual fish in samples of mixed populations. However, using several characters and comparing data from same year-classes, this method can undoubtedly prove successful in determining the various populations present in an area of mixing.

This report present some results of such analyses carried out on the autumn spawning group of herring in the northeastern North Sea during the years 1961—63.

The origin of this herring has been investigated by comparing meristic characters with those of the Kattegat autumn spawning stock and the «Bank» and «Downs» stocks.

MATERIAL AND METHODS

Twentythree samples were collected from September 1961 to May 1963. Most of the material originate from commercial catches, but 6 samples were collected onboard research vessels.

Otolith characters were used to separate spring and autumn spawned herring (Parrish and Sharman 1958). This procedure left 2 632 autumn spawners to be studied.

Sampling localities, gears and proportion of spring and autumn spawners are given in Table 1. There was no trend in length composition of the herring taken by different gears, and the samples are, therefore, presumed to give a fairly correct picture of the exploited stocks in the northeastern North Sea.

All the herring were examined as to age, number of vertebrae and stage of maturity. Both scales and otoliths were used for age determinations. Stage of maturity were dertermined according to the maturity scale recommended by the ICES Herring, Committee in 1962 (Anon. 1963).

The first growth zone measurement in otoliths and the l_1, l_2 and l_3 lengths were determined for a part of the material. The first growth zone in otoliths was measured from the centre of the opaque nucleus to the distal edge of the first winter ring, along an axis to the post-rostrum. The growth of the herring was estimated by back calculations of scales and applying the modified growth formula by Lea (1938).

Table 1. Sampling localities and composition of spring and autumn spawned herring in the samples (%) from north-eastern North Sea, 1961—63.

Sample number	Date	Locality	Gear	Spring spawners	Autumn spawners	Uncer-tain	N
1	11/ 9—61	N 59°00' E 03°00'	Trawl	11.3	84.1	4.5	88
2	24/ 9—61	N 58°55' E 03°09'	Trawl	9.0	86.0	5.0	100
3	16/10—61	N 59°20' E 03°00'	Trawl	11.0	86.5	2.5	200
4	19/12—61	N 59°00' E 03°00'	Trawl	13.5	82.0	4.5	200
5	19/12—61	N 59°08' E 03°10'	Trawl	19.0	76.0	5.0	200
6	19/ 1—62	N 58°07' E 04°36'	Trawl	18.4	78.4	3.2	250
7	20/ 1—62	N 59°00' E 03°30'	Trawl	24.4	72.0	3.6	250
8	1/ 3—62	N 59°45' E 03°35'	Drift	44.7	50.5	4.7	190
9	24/ 3—62	N 60°20' E 01°50'	Trawl	4.6	89.3	6.1	197
10	6/ 5—62	N 58°01' E 05°15'	Drift	22.0	61.0	17.0	100
11	7/ 5— 62	N 57°42' E 05°55'	Drift	16.7	68.7	14.7	150
12	22/ 5—62	N 60°00' E 03°20'	Trawl	15.0	83.0	2.0	100
13	7/ 6—62	N 59°00' E 03°34'	Trawl	15.3	81.3	3.3	150
14	27/ 7—62	N 59°45' E 00°16'	Trawl	70.7	24.7	4.7	150
15	28/ 8—62	N 57°55' E 04°50'	Drift	55.3	26.0	18.7	150
16	3/ 9—62	N 59°47' E 01°35'	Trawl	78.0	17.5	4.5	200
17	25/ 9—62	N 58°06' E 05°14'	Drift	19.0	76.0	5.0	100
18	9/10—62	N 57°50' E 05°40'	Drift	45.3	50.0	4.7	150
19	28/11—62	N 57°43' E 05°22'	Drift	20.0	72.5	7.5	200
20	22/ 1— 63	N 58°40' E 03°40'	Trawl	23.0	66.0	11.0	200
21	20/ 2—63	N 58°20' E 04°04'	Trawl	15.5	81.0	3.5	200
22	23/ 3—63	N 60°05' E 03°30'	Trawl	3.0	90.5	6.1	200
23	3/ 5—63	N 60°28' E 04°18'	Purse-seine	11.0	82.0	7.0	100
Total				25.0	68.8	6.2	3 825

The quality of the herring examined varied between samples. Except the 6 samples taken onboard research vessels, the samples were from 2 to 10 days old before examination. These samples had either been on ice or been frozen. No adjustments for shrinkage in length for these herring were made.

Frozen material may also give some inaccuracy in the maturity determination. Especially do the eggs tend to get hyaline after being frozen. The amount of hyaline eggs is the main character when distinguishing between the maturity stages IV and V and between the stages V and VI. Owing to diffuse limits between the different stages it is impossible to adjust these data.

RESULTS AND DISCUSSION

AGE COMPOSITION

According to Dahl (1907), Clark (1933), Hodgson (1934) and Wood (1951) the formation of the scales begin when the young herring is about 4—5 cm in length, which is approximately the size increment of the autumn hatched herring during the autumn and winter months. The first winter ring on the scales therefore will reflect the second winter condition. The validity of age determination has previously been discussed by Andersson (1946).

He suggested that some «Bank» herring hatched in August might lay down a winter ring at an age of three to four months, thus giving a group of herring whose age was overestimated by one year. The scales of these herring had a small size of the central area. No such scales were observed in the present material, and from information about the growth rate of larval and post larval herring it seems unlikely that substantial numbers of herring will lay down a winter ring during the first winter, as proposed by Andersson.

The otoliths, on the other hand, are present from the larval stage onwards. Herring hatched between August and January will lay down otoliths in winter condition, and consequently get otoliths with a hyaline nucleus.

The number of winter rings on the scales were always in accordance with those on the otoliths (outside the nucleus), which again demonstrates that the first winter ring on the scales is formed during the second winter. Not all scales and otoliths were suited for age determination, mainly due to secondary rings within the summer growth zones, regenerated scales and transparenty otoliths. A following scale for readability of scales and otoliths has been used:

Table 2. Percentage distribution of readability 0—4 of scales and otoliths of autumn spawned herring from northeastern North Sea, 1961—63.

		Readability					N
		0	1	2	3	4	
Trawl	Scale	36.2	9.1	4.6	26.8	23.3	1 953
	Otolith	69,8	9.2	9.6	11.4	0.1	1 953
	S+O[2])	77.7	9.1	6.7	6.6	—	1 953
Drift net	Scale	60.8	11.8	7.9	18.2	1.3	595
	Otolith	73.8	11.4	8.4	6.4	—	595
	S+O	85.2	8.1	4.0	2.7	—	595
Purseseine	Scale	59.8	11.0	12.2	17.1	—	82
	Otolith	65.9	13.4	8.5	12.2	—	82
	S+O	78.0	11.0	6.1	4.9	—	82
Total	Scale	45.2	9.8	5.6	24.6	17.6	2 630
	Otolith	70.6	9.8	9.3	10.3	+[1])	2 630
	S+O	79.4	8.9	6.1	5.6	—	2 630

[1]) < 0.05, [2]) scale and otolith combined.

0: certain
1: fairly certain, deviation of one year may occur.
2: uncertain.
3: regenerated scales, transparency otoliths, scales and otolith did not fit for age determination.
4: scales and otoliths lacking.

Table 2 summarizes the results of the observations on readability of scales and otoliths. The trawl and driftnet herring were frequently lacking scales, or the remaining scales were small and were not suited for age readings, which may explain the great discrepancy of the readability 0 for these gears. The percentage of readability 0 for the otoliths was high for all gears, and this investigation suggests that the otoliths are more suitable than scales for age determination. However, a reservation must be taken when the samples are dominated by older year-classes. Otoliths of autumn spawners were frequently impossible to read when dealing with herring of more than eight years.

The age determination of the samples is based upon readability 0 for either scales or otoliths. In this way positive age determinations were achieved for about 80 per cent of the material. The remaining 20 per cent of the material was most likely dominated by older herring, and this infers that the age composition of the samples is slightly biased

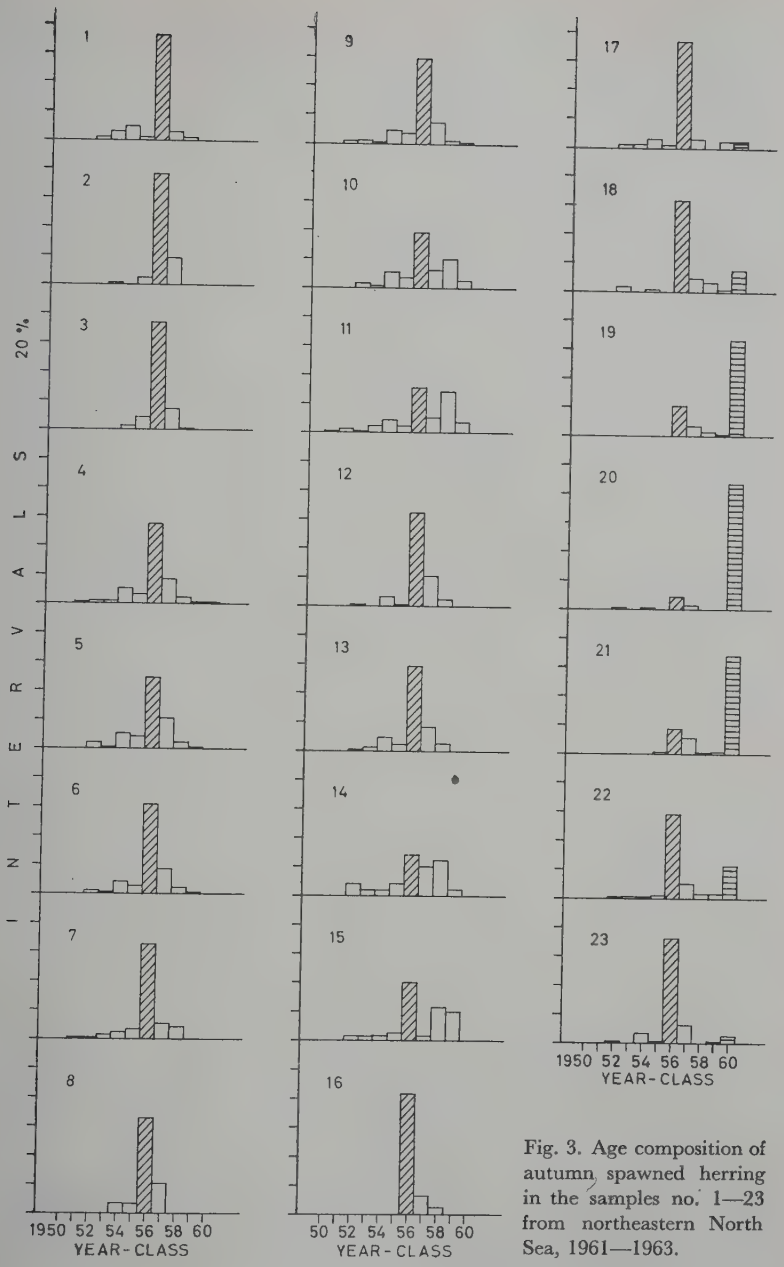

Fig. 3. Age composition of autumn spawned herring in the samples no. 1—23 from northeastern North Sea, 1961—1963.

(Fig. 3). The age composition in the samples from September 1961 to April 1962 is characterized by a strong 1956 year-class and comparatively strong 1954 and 1957 year-classes. During summer some of the samples from the southern and western part of the area (samples No. 10, 11, 14, 15) contained a higher admixture of younger year-classes, while the age composition in the northern part (samples No. 12, 13, 16) remained unchanged. From end of September 1962 the age composition changed considerably, due to a heavy inflow of two year old herring. This 1960 year-class did, however, not increase in abundance north of latitude 59°N.

Although the samples are few, and the number in some cases is low, the material may permit some tentative conclusions. The homogenous age composition of the autumn spawning group during autumn and winter 1961/1962 (September to April) may indicate that the area was visited by a single stock. The change of age composition in the region south of latitude 59°N during spring and summer (April to September) was probably caused by a segregation or an immigration of herring. Since the catches went down during this period the former explanation seems most reasonable. Members of a year-class first recruit the southern part of the region in autumn at an age of two years, and they will during the following winter mainly be distributed south of latitude 59°N.

In Fig. 4 is given the age composition of herring from the western, the central and the southern part of the North Sea. The material from the Bressay Shoal and the Fladen Ground is supposed to be representative

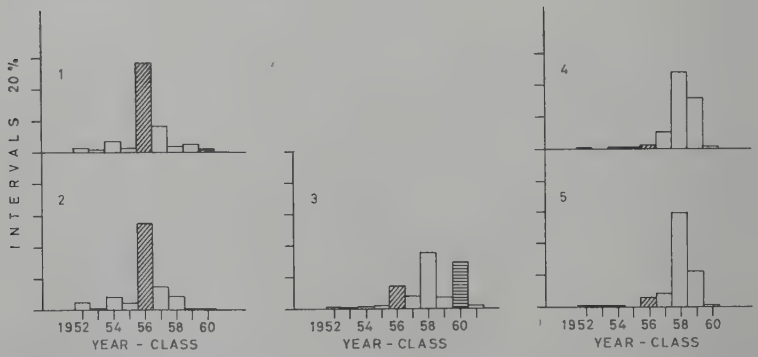

Fig. 4. Age composition of herring from western, central and southern part of the North Sea in 1962. 1) Bressay Shoal, June—Aug., N = 665, 2) Fladen Ground, July -Sept., N = 470, 3) Dogger Bank, Aug.—Oct., N = 4.297, 4) Sandettié, Nov.—Dec., N = 501, 5) Channel, Nov.—Dec., N = 485.

for the age composition of the «Bank» herring, and the material from Sandettié and Channel the «Downs» herring. The Dogger Bank area is during autumn supposed to be a mixing area of spawning «Bank» herring and mature «Downs» herring. This comparison shows a striking resemblance between the «Bank» herring and the autumn spawners in the northeastern North Sea during autumn and winter 1961/62 and during winter 1963 (north of latitude 59°N). Further, Fig. 4 shows that the 1958 year-class, which was dominating the «Downs» herring, also was abundant in some of the samples from spring and summer 1962 in the southern part of the investigated area.

In 1963 the age composition on the spawning grounds in western and southern part of the North Sea changed as a consequence of the strong 1960 year-class. The 1960 year-class constituted this year about 80 % and 70 % of the «Bank» and «Downs» stocks respectively (Saville, McPherson and Parrish 1965 and Gilis 1965). There is no information of the age composition of the Kattegat autumn spawners in 1962, but in autumn 1963 the 1960 year-class contributed about 90 % of this stock (Höglund 1965).

Due to the strength of the 1960 year-class in all autumn spawned herring, it is impossible to identify the various stocks in the northeastern North Sea south of the latitude 59°N during autumn and winter 1962/1963 by means of the age composition.

VERTEBRAE

The vertebral number is one of the most common characters used in distinguishing different herring stocks. This character is probably phenotypic, and the observed differences in mean vertebrae number between different stocks may be attributed to environmental conditions on the the spawning grounds.

In an area where different herring stocks are mixing it is reasonable, to assume that the mean vertebral number will fluctuate in proportion to the abundance of the different stocks.

In Table 3 are given the frequency distributions of the vertebrae counts of the sampled herring. The means varied between 56.35 and 56.66, but no trend in time and space was observed. An analysis of variance has been applied, and the result showed that the differences of vertebrae count within samples were insignificant compared with the differences between means of samples (Table 4). Consequently, one may consider the samples to be drawn from the same stock or same mixture of stocks. This assumption presupposes, however, that there is a real difference in vertebrae number between the various autumn spawning

Tabell 3. Vertebrae number in autumn spawners from northeastern North Sea, 1961—63.

Sample number	Date	Vertebral number							N	$\overline{\times}$ [1])	σ^2
		53	54	55	56	57	58	59			
1	11/ 9—61	—	—	3	24	42	5	—	74	0.6622	0.4459
2	24/ 9—61	—	—	1	39	44	2	—	86	0.5465	0.3213
3	16/10—61	—	—	3	82	84	4	—	173	0.5145	0.3326
4	19/12—61	—	—	4	72	86	2	—	164	0.5244	0.3245
5	19/12—61	—	—	5	69	75	2	1	152	0.5066	0.3841
6	19/ 1—62	—	—	4	78	101	13	—	196	0.6276	0.4093
7	20/ 1—62	1	1	4	78	87	9	—	180	0.5333	0.4961
8	1/ 3—62	—	—	2	35	51	7	—	95	0.6632	0.4172
9	24/ 3—62	—	1	7	69	95	3	—	175	0.5257	0.4002
10	6/ 5—62	—	—	2	32	23	4	—	61	0.4754	0.4536
11	7/ 5—62	—	—	6	49	38	8	—	101	0.4752	0.5319
12	22/ 5—62	—	—	6	46	27	4	—	83	0.3494	0.4740
13	7/ 6—62	—	—	4	66	48	3	1	122	0.4344	0.4130
14	27/ 7—62	—	—	—	19	15	1	—	35	0.4857	0.3160
15	28/ 8—62	—	—	2	21	13	2	—	38	0.3947	0.4616
16	3/ 9—62	—	—	1	19	14	1	—	35	0.4286	0.3697
17	25/ 9—62	—	—	1	38	35	1	—	75	0.4800	0.3070
18	9/10—62	—	—	—	33	39	3	—	75	0.6000	0.3243
19	28/11—62	—	—	4	63	64	7	—	138	0.5362	0.4111
20	22/ 1—63	—	—	6	57	65	4	—	132	0.5076	0.4045
21	20/ 2—63	—	—	4	70	79	6	1	160	0.5625	0.4112
22	23/ 3—63	—	—	8	81	86	5	—	180	0.4889	0.3965
23	3/ 5—63	—	—	2	40	35	4	—	81	0.5062	0.4031
Total		1	2	79	1 180	1 246	100	3	2 611	0.5243	0.4028

[1]) $\overline{\times}$ = average excess above the «working mean», 56 vertebrae.

Table 4. Analysis of variance of vertebrae number.

Source	Sum of squares	Degrees of freedom	Mean squares	
Within samples	11.5301	22	0.5241	$F = 1.3047$
Between means of samples.....	1039.7032	2 588	0.4017	$P < 0.05$
Total	1051.2333	2 610		

stocks. Earlier investigations have shown that the mean vertebrae number has an increasing trend from north to south, with low values on the Buchan spawning grounds and high values on the Sandettié and English Channel spawning grounds.

According to Anon. (1961) no large difference in mean vertebrae number was found between pre-and post-war investigations on «Downs» herring, and for the period 1952—1959 their means ranged from 56.53 to 56.59.

The mean vertebrae count of herring from the Dogger area varied in the period 1952—1959 between 56.51 and 56.56 with an overall mean of 56.55 (Anon. 1961). This figure is significantly higher than pre-war observations (Wood 1936). The spawning herring in the Buchan area had in pre-war years a mean vertebrae number of 56.42. During the years 1952—1955 the mean number was slightly different from pre-war data, but after 1955 the vertebrae number had a marked rise and up to 1960 the means ranged from 56.54 to 56.58 (Anon. 1961).

The Kattegat autumn spawners had in 1915 and 1922 a mean vertebrae number of 56.35 and 56.11 (Johansen 1924). The vertebrae number for this stock in recent years is unkonwn. The low means in some of the samples from summer 1962 can however, indicate an admixture of this stock in the northeastern North Sea.

The total mean vertebrae number (56.52) in the sampled material was in good agreement with those for the «Bank» and «Downs» stocks, and it may be concluded that these stocks, without intimate anything about the mutual abundance, inhabited the northeastern North Sea and constituted the dominant part of the autumn spawning group.

MATURITY

Fig. 5 shows the percentage frequency distribution of the maturity stages among the autumn spawned herring. The samples were collected throughout the year and it is suggested that this figure gives fairly coherent picture of the maturity cycle for the autumn spawning group of herring.

Transistional cases between two stages have been included under the higher stage. Difficulties in distinguishing between stage VIII and an advanced stage II occured frequently. Especially for herring which had spawned only once, criteria such as striation of gonad walls and size of blood vessels were not distinct, and these herring could therefore be confused with herring in stage II. In these doubtful cases the amount of

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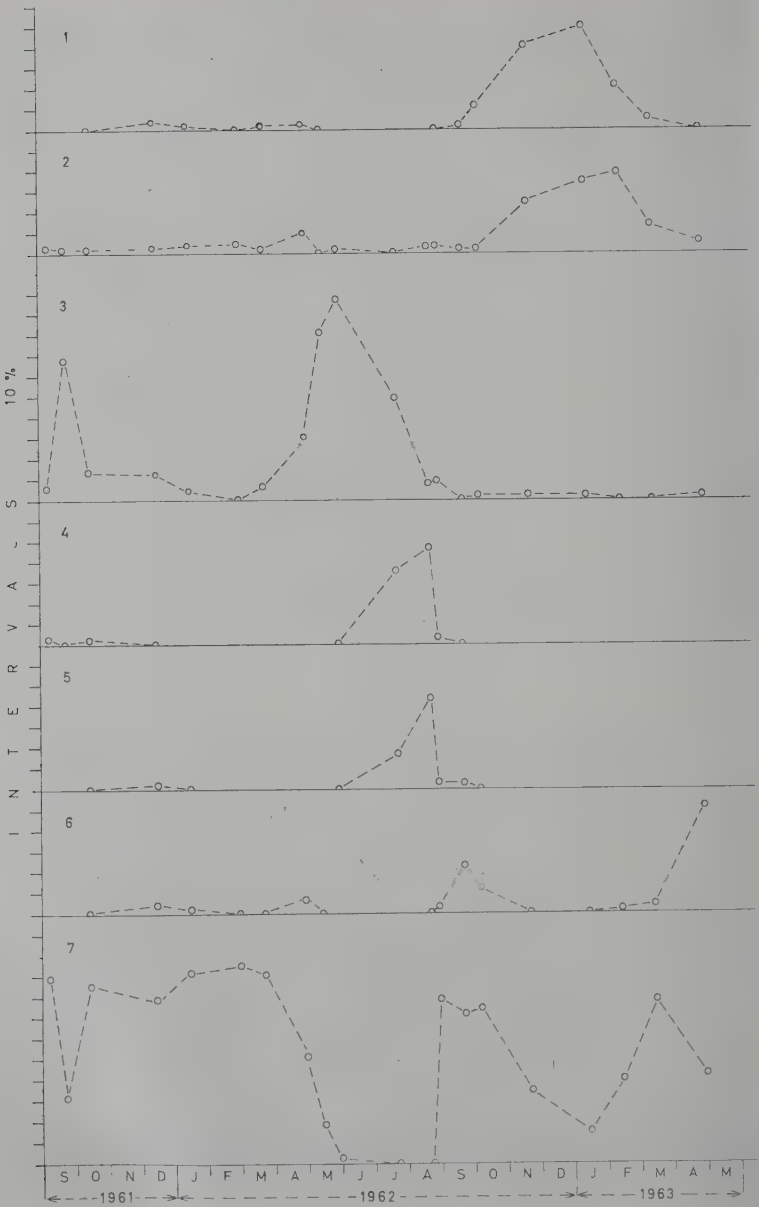
Fig. 5. Percentage composition of maturity stages in autumn spawned herring from northeastern North Sea, 1961—1963. 1) maturity stage I, 2) maturity stage II, 3) matiruty stage III, 4) maturity stage IV, 5) maturity stage V, 6) maturity stage VII, 7) maturity stage VIII.


1
2
3
4
5
6
7
10 %
INTERVALLS
S O N D J F M A M J J A S O N D J F M A M
1961
1962
1963

intestinal fat have been decisive; e.g. herring with moderate or large quantities of fat were determined to belong to stage II and herring with no or little fat, were determined to belong to stage VIII.

Immature herring, stages I and II, were scarce in the material up to October 1962. During autumn and winter 1962/1963 however, these stages dominated the samples due to the immigration of the strong 1960 year-class. Stage III occured in most of the samples, but were predominant in September 1961 and in May, June and July in 1962. The stages IV and V were present during July and August with maximum in second half of August. Due to emigration of mature herring from the northeastern North Sea to the spawning grounds during summer and early autumn these stages will probably cover a longer period than indicated in Fig. 5.

Spent herring, stage VII, were represented during December and January 1961/1962, and during September and October 1962. This fact points to an immigration of late and early autumn spawning components. From Fig. 5 it is noticed that stage VII also was present during spring in 1961 and 1962, which may indicate an alternation of the spawning season for these herring. According to Parrish and Sharman (1958) a small number of herring with «summer-autumn» characters in the otoliths have been recorded in spawning condition in spring in the Firth of Forth and the North Minch areas. There is also observations of spawning herring in August with distinct and definite «winter-spring» otoliths in an inlet on the west coast of Norway. Racial characters as scale pattern, l_1, vertebral number of these herring were in agreement with the Norwegian spring spawning stock. An alternation of the spawning season may therefore occasionally occur, but on the other hand, if a part of the autumn spawned herring in the northeastern North Sea have changed their spawning season, this should be reflected in a two-peaked curve of the various maturity stages.

The samples collected in spring and containing stage VII, had all been frozen and were in bad condition when examined. It seems most likely, therefore, that the maturity determination of these samples must be erroneous.

The maturity cycle of the autumn spawning group in the northeastern North Sea is characterized by a long duration of the recovering stage VIII, almost 8 months, and a rapid maturation during spring and summer. Stage VIII passes into stage III at the beginning of May.

According to Iles (1964) the timing of the onset of the maturation cycle varies little as does the time spent in the earlier maturation stages for the various autumn spawning stocks in the North Sea.

Spent and recovering herring in September and first half of October

belong probably to the «Bank» herring, but otherwise it seems impossible to distinguish between the various autumn spawning stocks by means of this characters.

AGE AT FIRST SPAWNING

The autumn spawners had no typical spawning rings on scales and otoliths. The age at first spawning has been based upon the maturity composition by age in the samples collected during autumn and winter.

Herring in stage III in this period are classified as uncertain, i.e. they may be immature and will not spawn before the next autumn, or they may have spawned and already recovered their gonads. The percentage composition of immatures (stages I and II), uncertain (stage III) and spent herring (stages VII and VIII) in each age group is illustrated in Fig. 6. It will be seen that first time spawners occured amongst two to six year old herring, but the majority of first time spawners, about 70 %, were spawning at an age of three. This feature is common, in the autumn spawning stocks in the North Sea and the Kattegat (Cushing and Burd 1957, Parrish and Craig 1957, Höglund 1965). The age at first spawning shows a marked change from the inter-war years, when only a small proportion of the herring matured as three years olds, and the major recruitment to the spawning shoals took place as four year old herring. The marked change in age at first spawning occured widely

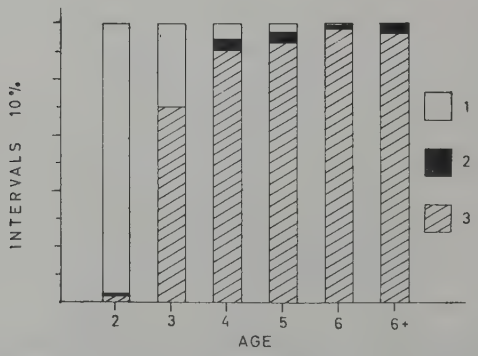


Fig. 6. Composition of immature herring, herring in maturity stage III and mature herring amongst 2—6 + year old autumn spawners from northeastern North Sea. 1) maturity stage I—II, 2) maturity stage III, 3) maturity stage IV—VIII.

over the North Sea in the early fifties and have been associated with an increase in growth rate during the adolescent and pre-recruit phases. This has resulted in an earlier movement from the nursery areas, and in an earlier maturation of herring recruiting both the «Bank» and «Downs» stocks (Burd 1962).

It should be noted that the average length by age decreased again in the southern North Sea between 1955 and 1961, but no obvious reversal of the recruitment pattern had taken place up to 1963.

OTOLITH TYPES

In recent years special attention has been paid by a number of herring workers to features of the herring otoliths (Einarsson 1951, Parrish and Sharman 1958, Postuma and Zijlstra 1958).

Parrish and Sharman (1958) found differences in the forms of the first winter zone and in the sizes of the first growth zone of members of the North Sea autumn spawning group. These features are probably phenotypic, but they may give some important hints to nursery areas from which herring of different spawning grounds are derived, and to a certain extent give information on the mixing of early and late autumn spawning herring. Two main types of otoliths were described:

1. Otoliths with a «wide» first winter zone and a relatively small first growth zone.
2. Otoliths with a «narrow» or a thin and sharp first winter zone and a relatively large first growth zone.

According to Das, Postuma and Zijlstra (1959) the «narrow» type was dominant amongst spawning herring in the Dogger Bank area, while the «wide» type was prominent on the spawning grounds in the southern North Sea and in the eastern part of the English Channel. On the Buchan spawning grounds the «narrow» type constituted a greater part than in the Dogger area (Parrish and Sharman 1959 a), and a decreasing trend of the «narrow» otolith type from north to south seemed to exist.

The occurence of the two otolith types in the samples from north-eastern North Sea is given in Table 5. This table also include otoliths which could not be categorized under either of these major types, and they contributed about 7 % of all the otoliths examined.

Table 5. Percentage distribution of otolith types amongst autumn spawners from northeastern North Sea, 1961—63.

Sample number	Date	«Narrow»	«Wide»	Uncertain	N
1.....	11/ 9—61	87.8	4.1	8.1	74
2.....	24/ 9—61	82.6	9.3	8.1	86
3.....	16/10—61	88.4	5.2	6.4	173
4.....	19/12—61	84.1	6.1	9.8	164
5.....	19/12—61	79.6	7.2	13.2	152
6.....	19/ 1—62	84.7	4.1	11.2	196
7.....	20/ 1—62	82.2	11.7	6.1	180
8.....	1/ 3—62	87.5	8.3	4.2	96
9.....	24/ 3—62	85.2	8.5	6.3	176
10.....	6/ 5—62	91.8	6.6	1.6	61
11.....	7/ 5—62	83.5	9.7	6.8	103
12.....	22/ 5—62	91.6	3.6	4.8	83
13.....	7/ 6—62	88.5	6.6	4.9	122
14.....	27/ 7—62	78.4	10.8	10.8	37
15.....	28/ 8—62	79.5	10.3	10.3	39
16.....	3/ 9—62	91.4	—	8.6	35
17.....	25/ 9—62	92.1	2.6	5.3	76
18.....	9/10—62	89.3	5.3	5.3	75
19.....	28/11—62	93.1	2.8	4.1	145
20.....	22/ 1—63	96.2	0.8	3.0	132
21.....	20/ 2—63	90.7	3.7	5.6	162
22.....	23/ 3—63	83.4	10.5	6.1	181
23.....	3/ 5—63	87.8	7.3	4.9	82
Total		86.8	6.4	6.8	2 630

From Table 5 it is seen that the «narrow» type dominated in all the samples, and no trend neither in time or in space was observed in the frequency of the two otolith types. It is interesting to note that the frequency of the «wide» otolith type either is increasing during the summer feeding season nor is decreasing during the spawning season for the «Downs» stock, which may indicate that members of this stock do not immigrate into the northeastern North Sea.

In Table 6 is given the percentage distribution of otolith types amongst age groups for the years 1961—1963. The most important features of these data are as follows:

1) «Wide» zoned otoliths were not found in the 2 year old herring.
2) The proportion of the two otolith types differed between year-classes. The 1958 year-class had a relatively high proportion of the «wide» type as three to six year olds.

Table 6. Percentage distribution of otolith types by age amongst autumn spawners in northeastern North Sea, 1961—63. (N = «Narrow» type, W = «Wide» type, U = unclassified.)

Year \ Age / Type	2			3			4			5			6			7			7+			N
	N	W	U	N	W	U	N	W	U	N	W	U	N	W	U	N	W	U	N	W	U	
1961	100	—	—	69	23	8	87	6	7	83	8	9	82	3	15	89	6	5	94	6		513
1962	99	—	1	92	4	4	83	12	5	82	10	8	86	8	6	96	4	—	83	6	1	1 101
1963	—	—	—	98	1	1	86	14	—	80	20	—	79	9	12	81	12	7	75	19	6	473

There was no evidence from the data of an increase in the proportion of «wide» otoliths with age as found by Parrish and Sharman (1959 b) in the northwestern North Sea. The high proportion of «narrow» typed otoliths in the samples suggests a connection between the «Bank» stock and the autumn spawning herring in the northeastern North Sea. However, it is impossible to verify this statement, as long as the otolith type composition amongst the Kattegat autumn spawning stock is unknown.

FIRST GROWTH ZONE MEASUREMENT ON OTOLITHS

The frequency distribution of first growth zone measurements for the two otolith types exhibited marked differences. The ranges and means for the «wide» and «narrow» types are presented in Table 7. The percentage frequency distributions for the two otolith types are illustrated in Fig. 7. It appears that the first growth zone measurements for «wide» type were smaller than for «narrow» type, and further, that the distributions and means within each type were similar in the years investigated. The high means for «narrow» type in samples no. 19—21 are probably caused by growth differences between year-classes. As mentioned before, the 1960 year-class dominated these samples, while the 1956 year-class was dominant in the others. Considering the total material the first growth zone measurements for «narrow» otoliths ranged from 20 to 39 units (one unit = 0.0409 mm), and had a mean value of 29.8 units. The corresponding figures for «wide» otoliths were 18—30 units and 24.6 units.

The ranges and means for the «narrow» and «wide» otoliths from northeastern North Sea were somewhat lower than the values obtained for the «Bank» herring in the years 1953—1956 (Parrish and Sharman 1959 b). These differences were, however, small and probably inside the expected range when dealing with material consisting of different year-classes.

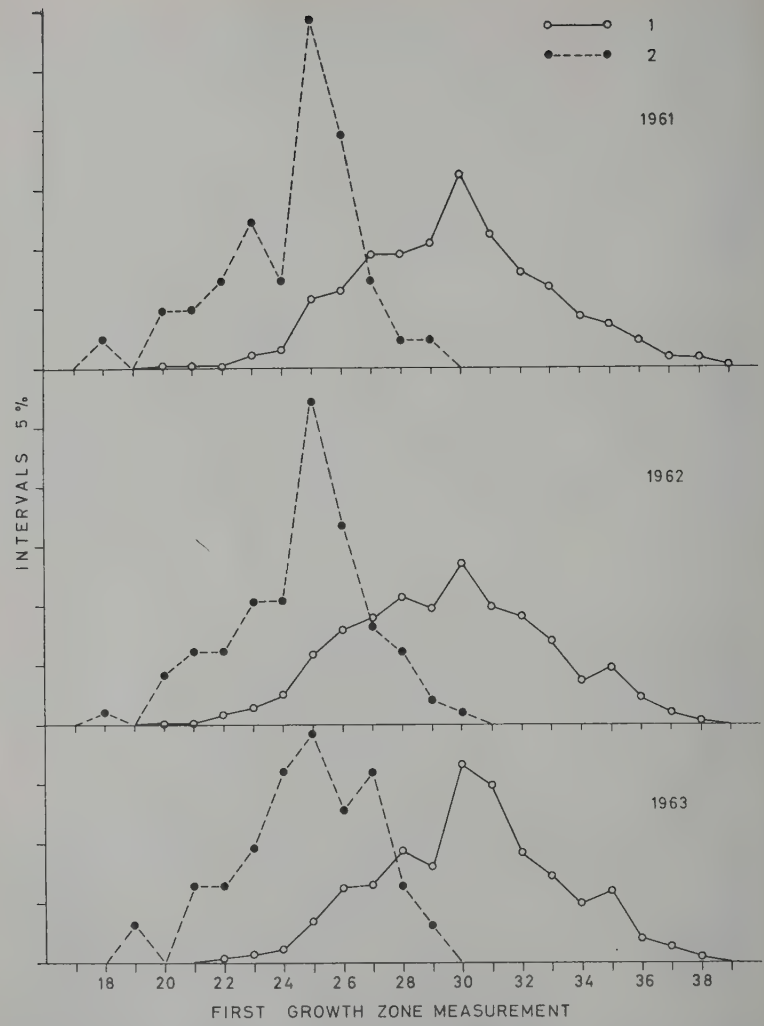


Fig. 7. Frequency distributions of otolith zone measurements of autumn spawned herring in north eastern North Sea, 1961—1963. 1) «narrow» otolith type, 2) «wide» otolith type.

Table 7. Ranges and means of first growth zone measurement on «narrow» and «wide» otolith types amongst autumn spawners from northeastern North Sea, 1961—63 (1 unit = 0.0409 mm).

Sample number	Date	«Narrow»			«Wide»		
		Range (unit)	Mean	N	Range (unit)	Mean	N
1.....	11/ 9—61	23—39	29.7	64	25—26	25.3	3
2.....	24/ 9—61	23—37	30.4	68	23—26	24.9	8
3.....	16/10—61	22—38	30.1	149	22—29	25.3	9
4.....	19/12—61	20—38	29.6	137	20—27	24.1	10
5.....	19/12—61	23—38	29.1	115	18—28	23.2	11
Sum 1961 .		20—39	29.8	533	18—29	24.4	41
6.....	19/ 1—62	23—37	30.0	159	23—29	25.1	9
7.....	20/ 1—62	22—38	29.7	144	20—29	25.5	21
8.....	1/ 3—62	21—37	29.1	81	20—30	23.9	8
9.....	24/ 3—62	23—38	29.7	146	22—28	25.3	15
10.....	6/ 5—62	22—36	29.0	56	21—26	23.3	4
11.....	7/ 5—62	22—38	29.2	82	20—26	23.0	10
12.....	22/ 5—62	22—38	29.2	74	21—26	23.1	3
13.....	7/ 6—62	22—36	28,8	108	22—27	24.4	8
14.....	27/ 7—62	22—35	28.2	28	24—25	24.8	4
15.....	28/ 8—62	24—33	27.8	31	18—26	23.3	4
16.....	3/ 9—62	26—36	30.0	31	—	—	0
17.....	25/ 9—62	20—37	29.3	69	25—26	25.5	2
18.....	9/10—62	23—37	30.2	65	24—28	26.3	4
19.....	28/11—62	22—37	31.0	129	21—27	24.3	4
Sum 1962		20—38	29.6	1 203	18—30	24.6	96
20.....	22/ 1—63	24—38	30.8	117	25	25.0	1
21.....	20/ 2—63	23—37	30.4	142	24—29	26.4	5
22.....	23/ 3—63	23—37	30.0	145	21—27	24.4	19
23.....	3/ 5—63	22—38	29.7	69	19—28	24.5	6
Sum 1963		22—38	30.3	473	19—29	24.8	31
Grand Total		20—39	29.8	2 209	18—30	24.6	168

In Table 8 is the present material compared with the means of the first growth zone measurements for the two otolith types amongst herring from the Dogger area (Bohl 1960). In both areas the 1956 year-class was dominating, as 2 year olds in the Dogger area and as 5—7 year olds in the northeastern North Sea.

Table 8. Mean first growth zone measurement (mm) on «narrow» and «wide» typed herring from Dogger Bank and northeastern North Sea.

Type	Dogger Bank	N	NE North Sea	N
«Narrow»	1.23	928	1.22	2 209
«Wide»	1.02	332	1.01	168

The good conformity indicates a connection between pre-recruits in the Dogger area and mature herring in the northeastern North Sea.

The result of this investigation provide some pointers to the supply and composition of the autumn spawners in the northeastern North Sea. However, at present it is not possible to assess the full biological significanse between the two otolith types and the usefulness of this character in herring «racial» studies. It is suggested that the differences between the growth zones of the «wide» and «narrow» types are due to an early or late time of hatching or to a difference in growth rate. The differences between the size of the first winter zone in the two otolith types are probably a result of growth and metabolism differences between herring inhabiting different areas.

It should also be noted that there was no differences in vertebrae number between «narrow» and «wide» typed herring. The frequency distributions of Vert.S. for the two types are given in Table 9 ($t = 0.8589$, $0.3>p>0.4$).

Before the usefulness of otolith features in herring «racial» studies can be assessed, more information of the otolith types amongst the spawners from the Dogger, the Southern Bight and the northern Kattegat areas are needed. Also extensive studies of herring in different nursery areas must be carried out, and the effect of food and temperature on ring formation should also be investigated.

Table 9. Vertebrae number of «wide» and «narrow» typed herring amongst autumn spawners from northeastern North Sea, 1961—63.

Type	Vertebral number						N	$\overline{\times}$ [1]	σ^2
	54	55	56	57	58	59			
«Wide» ...	—	5	75	85	1	—	166	0.4940	0.3242
«Narrow» .	2	63	1 023	1 082	93	3	2 266	0.5340	0.3999

[1] $\overline{\times}$ = average excess above the «working mean», 56 vertebrae.

GROWTH

Lea (1910, 1938) has shown that the relation between scale length and total length of the herring is approximately linear. The differences in spawning time and nursery areas between the various stocks are assumed to be reflected in the l_1 values, and the l_1 distributions have been one of the main characters used for identifying herring in mixing areas. In the North Sea the differences of the l_1 distributions between the «Bank» and «Downs» herring are clearly demonstrated by Burd (1962). Burd also showed that the differences between the l_1 distributions of «Bank» and «Downs» herring were much greater than the differences between year broods and the differences within a year brood.

The l_1 distributions have been obtained by projection and proportioning the scales of six year old herring (1956 year-class). For calculating the l_1 values, the modified growth formula of Lea (1938) was applied

$$l_1 = \frac{s_1}{S_n} L + \left[1 - \frac{s_1}{S_n}\right]$$

where s_1 and S_n refer to measurements on the scale from the basal line to the first winter-ring and the edge respectively, L is the total length of the fish, l_1 is the calculated length at the formation of the first winter-ring. The obtained data are illustrated in Fig. 8, and for comparison is shown the l_1 distribution of four year-olds (1954 year-class) «Bank» and «Downs» herring (Anon. 1962, Burd 1962). A weakness with this comparison is that different year-classes are compared and that the l_1 data are based upon different growth formulas. The l_1 data for the «Bank» and «Downs» herring in Fig. 8 are calculated by Lea's first formula, i.e. these data are in average $\left[1 - \frac{s_1}{S_n}\right]$ cm lower than the l_1 data presented for the autumn spawners in northeastern North Sea.

The differences in growth by using the two formulas are for 6 year old herring estimated to be 0.5 cm. Notwithstanding this disadvantage, it is concluded that there is good agreement between the l_1 data for the autumn spawning herring in the northeastern North Sea and the «Bank» herring stock.

The differences found in first growth zone measurements in the «narrow» and «wide» typed herring suggest that similar differences would be found in the l_1 data of these two groups of fish. In Fig. 8 is also the l_1 distribution separated on otolith types. The good correspondance, when comparing with the l_1 data for the «Bank» and the «Downs» herring could indicate that the «wide» type was originating from the «Downs» stock and the «narrow» type from the «Bank» stock. Good

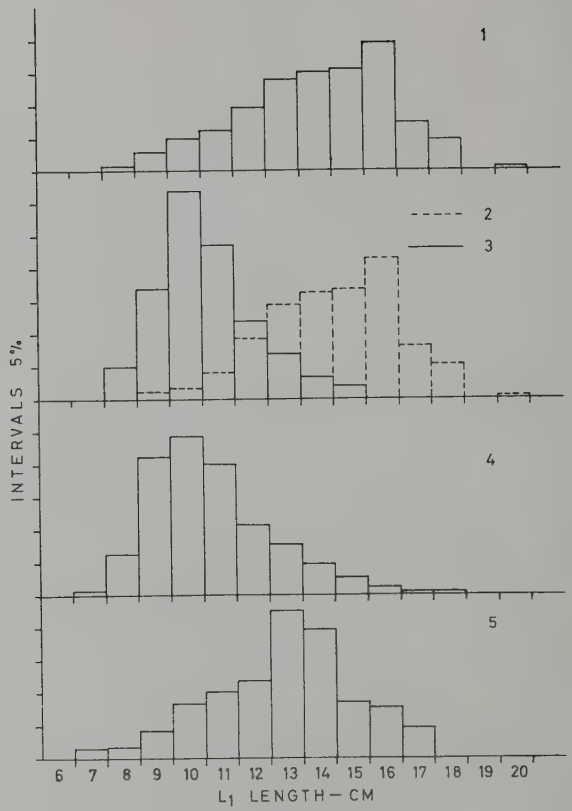


Fig. 8. Frequency distribution of l_1 for 6 year old (1956 year-class) autumn spawned herring (also separated in «narrow» and «wide» types) in northeastern North Sea, compared with the l_1 distribution for 4 year old (1954 year–class) «Bank» and «Downs» herring. 1) Autumn spawned herring northeastern North Sea, 2) «Narrow» typed herring northeastern North Sea, 3) «Wide» typed herring, northeastern North Sea, 4) «Downs» herring, 5) «Bank» herring.

Table 10. The length (l) of 1, 2, ... 5 year-old «narrow» and «wide» typed herring amongst autumn spawners from north-eastern North Sea.

A. «Narrow» type.

Year-class	l_1 cm			l_2 cm			l_3 cm			l_4 cm			l_5 cm		
	Mean	$\pm \frac{2\sigma}{\sqrt{N}}$	N	Mean	$\pm \frac{2\sigma}{\sqrt{N}}$	N	Mean	$\pm \frac{2\sigma}{\sqrt{N}}$	N	Mean	$\pm \frac{2\sigma}{\sqrt{N}}$	N	Mean	$\pm \frac{2\sigma}{\sqrt{N}}$	N
1960	16.79	0.30	99	—	—	—	—	—	—	—	—	—	—	—	—
1959	16.13	2.02	4	24.50	—	1	—	—	—	—	—	—	—	—	—
1958	16.50	0.98	11	23.31	1.32	8	25.25	0.50	2	—	—	—	—	—	—
1957	15.31	0.45	58	22.38	0.34	52	25.51	0.23	52	27.10	0.36	10	—	—	—
1956	14.77	0.31	171	22.56	0.23	154	25.45	0.18	153	26.85	0.15	135	28.11	0.51	35
Total	15.51	0.22	343	22.56	0.19	215	25.46	0.14	207	26.87	0.14	145	28.11	0.51	35

B. «Wide» type.

Year-class	l_1 cm			l_2 cm			l_3 cm			l_4 cm			l_5 cm		
	Mean	$\pm \frac{2\sigma}{\sqrt{N}}$	N	Mean	$\pm \frac{2\sigma}{\sqrt{N}}$	N	Mean	$\pm \frac{2\sigma}{\sqrt{N}}$	N	Mean	$\pm \frac{2\sigma}{\sqrt{N}}$	N	Mean	$\pm \frac{2\sigma}{\sqrt{N}}$	N
1960	15.50	—	1	—	—	—	—	—	—	—	—	—	—	—	—
1959	12.50	—	1	22.00	—	1	—	—	—	—	—	—	—	—	—
1958	12.17	1.01	12	20.55	1.15	11	24.25	1.16	8	—	—	—	—	—	—
1957	12.59	0.67	17	20.84	0.35	16	24.63	0.28	15	26.17	0.33	3	—	—	—
1956	10.96	0.39	60	19.28	0.37	59	23.42	0.27	50	25.37	0.26	53	26.66	0.40	22
Total	11.49	0.36	91	19.76	0.33	87	23.73	0.25	81	25.41	0.25	56	26.66	0.40	22

correlation between l_1 and otolith types have also been found by RATTY (1961), who estimated a critical length at 11.5 cm for formation of «narrow» and «wide» otoliths, i.e. herring longer than 11.5 cm in the second winter would lay down a «narrow» ring and herring smaller than 11.5 cm a «wide» ring. The proportion of herring longer and smaller than 11.5 cm in the «Bank» and «Downs stocks will differ by virtue of the 3—6 months difference in spawning time, and consequently the composition of otolith types in the two stocks will also be different. On this basis a comparison between l_1 of «wide» typed herring and «Downs» herring (where «wide» type is dominating) and between l_1 of «narrow» typed herring and «Bank» herring (where «narrow» type is dominating) will always give good conformity.

The two otolith features point to the presence of distinct nursery areas for the smaller and larger herring during their second winter. By analogy with the origins of «northern» and «southern» scale types identified by LEA (1929) it is probably that the «narrow» zoned type are from a colder second winter nursery area than the «wide» zoned type.

A difference of nearly 4 cm between modal length at formation of the first winterring of these two groups of fish is suggested to be so much that they will maintain a difference in growth throughout their life. The resulting data of backcalculation of «narrow» and «wide» typed herring are summarized in Table 10, giving the mean values of $l_1, l_2, \ldots . l_5$ and their standard errors for the various year-classes. From this table it is clear that the «narrow» and «wide» typed herring differed in growth rate. Mean lengths by age were significant higher for all age groups amongst the «narrow» typed herring. The difference in growth between the two types of herring may well be attributable to the original difference in l_1. The «narrow» and «wide» herring are probably, as suggested above, both belonging to the «Bank» herring stock. The good comformity in growth between the «wide» typed herring in the present material and the «Downs» herring may, however, indicate that this component have some similarities with the «Downs» stock, such as nursery areas, feeding grounds or feeding times.

CONCLUDING REMARKS

To outline the origin of the autumn spawning group of herring in the northeastern North Sea, some biological characters for this group of herring have been compared with the «Bank», the «Downs» and the

Kattegat autumn spawning stocks. Due to the plasticity in these characters and the large degree of overlap of values between the stocks it is difficult to attain a complete identification of the herring by this method. However, using several characters this method may give valuable pointers to the stock composition within the autumn spawned herring in this part of the North Sea.

The age composition in the samples from September 1961 to May 1962 showed a striking conformity with the «Bank» herring stock (Fig. 4). According to otolith type composition (Table 5) and the Vert. S. (Table 3) in these samples it seems obvious that the intermingle of herring from other stocks was negligible during that period.

In the samples from May to September 1962 it was more difficult to identify the stock composition. The samples during this period had a low first growth zone measurement in the «narrow» otoliths (Table 7) together with low values of Vert. S. (Table 3). These changes could be a consequence of a segregation, i.e. the older year-classes have emigrated from the area, resulting in a stronger dominance of the 1958 and 1959 year-classes (Fig. 3), or an immigration of other herring stocks had taken place. An analysis of variance of Vert. S. showed that the differences within year-classes were insignificant compared with the differences between year-classes. It should, however, be noted that the 1958 and 1959 year-classes had the lowest values of Vert. S., with means of 56.467 (60) and 56.368 (19) respectively. Due to the low values of Vert. S. and the high proportion of «narrow» typed otoliths (Table 5) it is suggested that the immigration of «Downs» herring to the north-eastern North Sea was negligible. One sample of Kattegat autumn spawners (kindly sent me by Dr. Höglund, Lysekil) had a high proportion of «narrow» typed otoliths (96.9 %) and a low first growth zone measurement (27.35 units). To what extent these values are representative for the Kattegat autumn spawners is unknown, but these values together with the low values of Vert. S. could indicate that the autumn spawned herring in the northeastern North Sea in the period May to September 1962 were mixed up with Kattegat autumn spawning herring.

During autumn 1962 the 1960 year-class immigrated the north-eastern North Sea south of latitude 59°N. This year-class proved to be strong amongst the «Bank», the «Downs» and the Kattegat autumn spawning stocks, but the high vertebral count (Table 3), the high proportion of «narrow» typed otoliths (Table 5) and the high valvues of the first growth zone measurement (Table 7) should argue for that the herring of this year-class in the northeastern North Sea mainly did derive from the «Bank» herring stock. North of latitude 59°N, however, there was during the winter 1963 a striking conformity in age composi-

tion, vertebral number, composition of «narrow» and «wide» typed otoliths between the sampled herring and the «Bank» herring stock.

From this investigation it is concluded that the autumn spawning group of herring in the northeastern North Sea is mainly constituted of the «Bank» herring stock. This stock is prevailing amongst the autumn spawning group of herring during autumn, winter and spring, but is during summer probably mixed up with Kattegat autumn spawners in areas south of latitude 59°N.

SUMMARY

1. The present report deals with the autumn spawning group of herring in the northeastern North Sea and an analysis of some biological characters as age composition, maturity cycle, otolith type composition, first growth zone measurement on otoliths and growth. The material consists of 23 samples, collected during the period September 1961 to May 1963.
2. The otoliths were more suitable than the scales for age determination. The 1956 year-class was dominating in the samples up to autumn 1962 in the whole area and also in the samples taken north of latitude 59°N during the winter 1963. In autumn 1962 the 1960 year-class immigrated the southern area and made up between 65—85 % of the autumn spawned herring.
3. An analysis of the vertebrae number showed that the differences of the variance within samples were insignificant compared with the differences between means of samples. The mean vertebrae number of the total material was 56.524 ($\pm$ 0.025).
4. The maturity cycle of the autumn spawned herring has been considered. The maturity stage VIII had a duration of about 8 months, and dominated the samples from September to May. Stage III dominated from mid May to the end of July. The stages IV and V were present during July and August with a maximum in the second half of August. Spawning of herring was not recorded in the area investigated.
5. An analysis of the composition of «narrow» and «wide» zoned otoliths showed that the proportion of «narrow» typed herring was in majority in all the samples and constituted 87 % amongst the autumn spawned herring.

6. Measurements of first growth zone in «narrow» and «wide» otoliths gave mean values of 29.78 ($\pm$ 0.14) and 24.59 ($\pm$ 0.35) units for the two types respectively (1 unit = 0.0409 mm).
7. The l_1 distribution and the mean lengths by age showed a significant difference between the «narrow» and «wide» typed herring in the northeastern North Sea. Both types of herring were most likely of the «Bank» herring stock.
8. The relationship between the autumn spawning group of herring in the northeastern North Sea and the «Bank», the «Downs» and the Kattegat autumn spawning stocks have been examined. The «Bank» herring evidently dominated the autumn spawning group during autumn, winter and spring. During summer, however, the autumn spawned herring in the areas south of latitude 59°N in the northeastern North Sea was probably mixed up with members of the Kattegat autumn spawning stock. The occurrence of «Downs» herring seemed to be lacking or negligible in the sampled material.

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INVESTIGATIONS ON HERRING, *CLUPEA HARENGUS L.*, FROM THE NORWEGIAN SKAGERAK COAST DURING THE YEARS 1963—64

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INTRODUCTION

A quite good herring fishery took place on the Norwegian Skagerak coast in the last part of the last century. The available data on the output of this fishery (Anon. 1884—1962) shows a rapid decrease in the inner part of the Norwegian Skagerak coast (Fig.1). After 1895 the catches were small except for a very short period about 1905. The fishery during the last war was also slightly better than usual, but in both cases considerably lower than during the good period in the previous century. A similar change has taken place in the fishery on the Swedish Skagerak coast (Andersson 1960). This fishery was to the turn of the century carried out in the skerries, and the most important gear was land seine and net. In this century the Swedish Skagerak fishery have mostly been an open sea fishery. According to investigations by Andersson (1958) it has since 1914 been based on North Sea autumn spawning, Kattegat autumn spawning and Skagerak spring spawning herring. Kattegat autumn spawners migrate as full herring from the North Sea to the Kattegat in late summer and form together with the Skagerak spring spawners the basis of the fishery in the first part of the season. From November—December most of the herring are North Sea autumn spawners which is the far biggest of the three races, but periodically the autumn spawners fail to appear.

On the Norwegian Skagerak coast the fishery in the last century started in November—December and lasted to February—March. There were no herring investigations in these years, and it is therefore not known which herring races the fishery was based on.

The fishery in the inner part of the Norwegian Skagerak coast now takes place in the skerries in late summer and autumn as a purse seine fishery with light. In the spring when only spring spawning herring are caught, net is the most important gear.

The present paper gives the results of an investigation on herring from the Telemark coast (Fig. 2) during the period July 1963—September 1964.

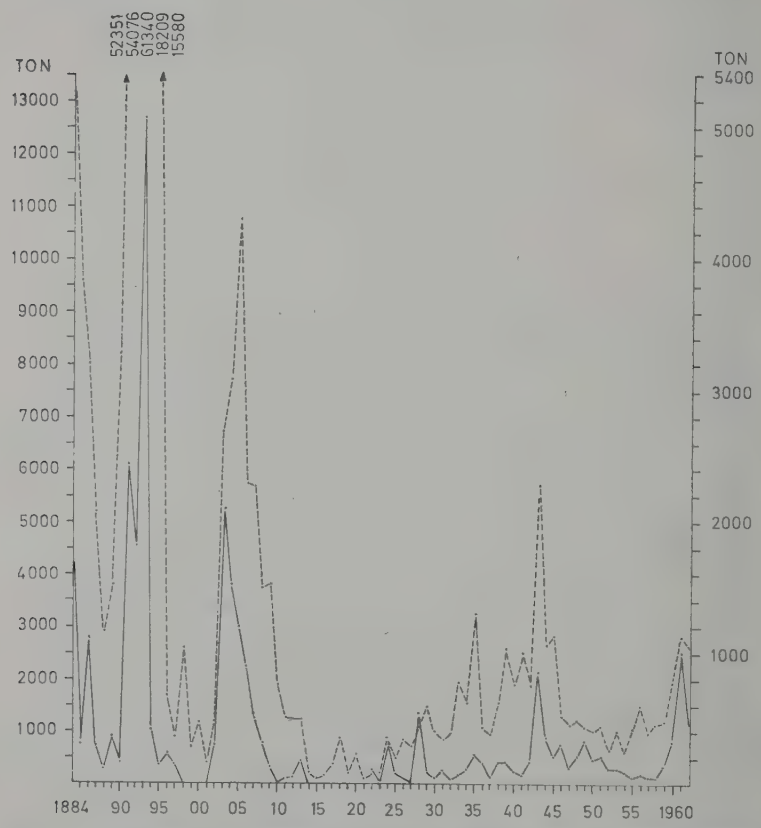


Fig. 1. Yearly output of the herring fisheries from 1884 to 1962. The inner Skagerak coast from the Aust-Agder border to the Swedish border (dotted lines). The Telemark coast (straight lines). The Skagerak coast (left scale). The Telemark coast (right scale).

MATERIAL AND METHODS

The material has been obtained from commercial catches taken in the fjords or between the skerries. The number of fish in the samples varied considerably, from 86 in sample no. 11 to 202 in sample

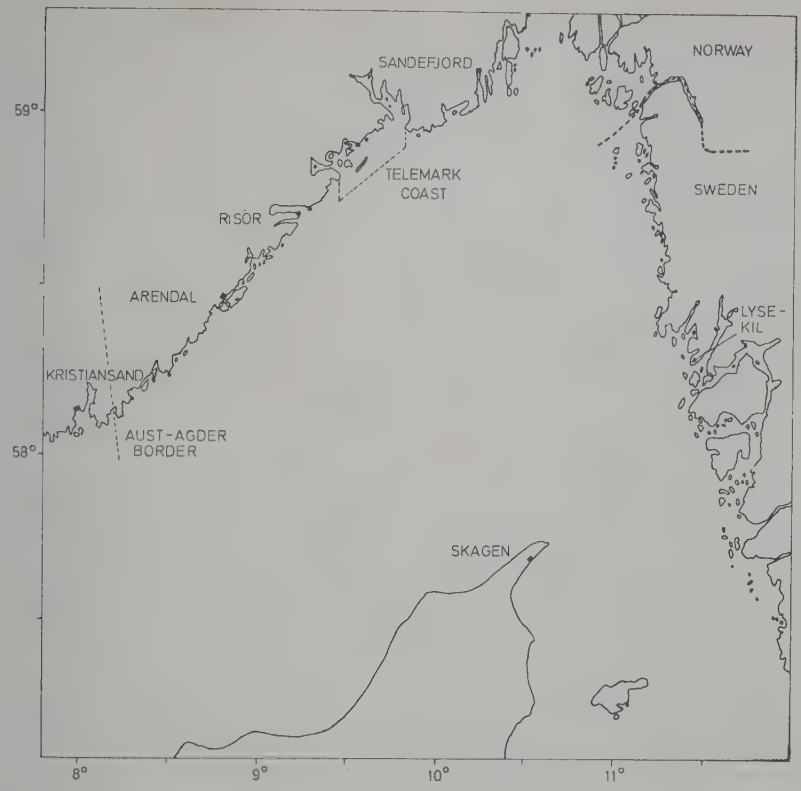


Fig. 2. The Skagerak coast.

Table 1. Mean vertebrae count, mean length and mean weight in the samples

Sample no.	Date	Vert. S.	Length	Weight	N
1	25/ 7—63	57.077	29.37	241.31	130
2	14/ 8—63	56.693*)	26.96	184.10	150
3	12/ 9—63	56.879	28.33	211.97	99
4	17/10—63	56.987	27.97	210.46	154
5	22/10—63	56.668*)	25.43	148.98	202
6	5/11—63	57.092	30.25	260.88	119
7	27/ 2—64	57.082	28.30	169.35	184
8	20/ 4—64	57.017	28.37	172.64	121
9	28/ 7—64	56.733*)	27.44	204.01	135
10	25/ 8—64	56.832*)	28.99	229.46	137
11	30/ 9—64	57.012	30.12	246.98	83

*) Samples tested not to be homogeneous according to the «Student-t» test.

no. 5 (Table 1). Efforts were made to obtain samples every month, but this was not possible. In the period July—November nine of the samples were taken, while only two were taken in the spring. In the samples no. 2 and 9 some herring were too damaged to be examined. The samples were taken from purse seine catches except samples no. 7 and 8 which were taken with nets.

The following data were collected from each individual: total length, weight, stage and weight of gonads, intestinal fat content, vertebrae number and scales. In addition otoliths were taken from the last 5 samples.

The total length of the fish was measured with the lobes of the tail in the mid line. The readings were made to the nearest half cm, using a measuring board with an offset of 0.25 cm.

Each individual has been weighed to the nearest 5 g and the gonads to the nearest 1 g.

The maturity stage of gonads was at first determined according to a scale introduced by Sivertsen (1937). However, during the investigations the scale with four stages proved to differentiate insufficient, and therefore the scale adopted by the ICES Herring Committee in 1962 (Anon. 1963) was applied from sample no. 7 onwards.

The content of the intestinal fat was determined after a scale with 4 stages used by Hjort (1914).

The otoliths were cleared in xylene for about half a minute (Parrish and Sharman 1958) and mounted on black plates.

The urostyle was included in the vertebrae count.

The growth was backcalculated from the scales according to the method introduced by Lea (1910). The lengths of l_1, l_2 etc. were grouped to the half cm below (Anon. 1963).

RESULTS

VERTEBRAE COUNTS

There were great variations in mean vertebrae number of the different samples (Table 1). The samples no. 7 and 8 were regarded as belonging to the same race as all the individuals were spawning. «Student-t» tests showed significant differences ($p > 0.05$) between the mean vertebrae number, 57.056, of the samples no. 7 plus 8 and the mean vertebrae number of the samples no. 2, 5, 9 and 10 (Table 1). It was therefore concluded that these four samples were mixtures of two or more races.

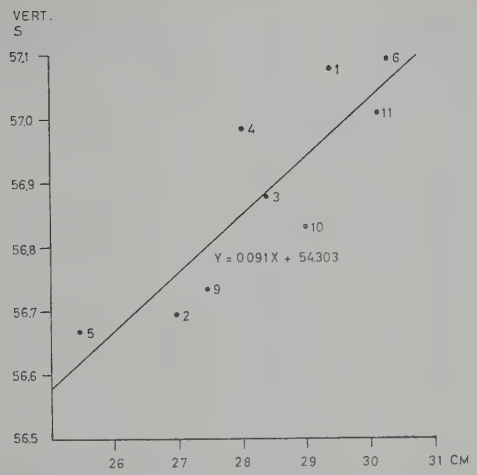


Fig. 3. Correlation between the mean length and the mean vertebrae count in the samples.

In Fig. 3 is showed the regression of mean lengths on mean vertebrae numbers (the samples no. 7 and 8 excluded), given by the equation:

$$y = 0.091\ x + 54.303$$

The correlation coefficient is 0.87. The equation is an approximate expression for the linear relationship between the length of individuals and vertebrae number. The figure indicates that the low vertebare number in the mixed samples are caused by small individuals.

Table 2 shows the mean vertebrae number in the different winter ring groups in the samples and indicates, though the number of individuals are small, that the herring with 2 winter rings have lower mean vertebrae number in the mixed samples (no. 2, 5, 9 and 10) than in the others.

AGE

Different herring races were expected to inhabit the investigated area. In Fig. 4 are shown the frequency distributions of winter rings inside the scale edge. These distributions are assumed to be similar to the age distributions, but small errors may occur. The autumn spawners may in some cases form scales the first winter (Andersson 1951), and therefore autumn spawners belonging to the same year-class may show a difference of one winter ring.

There were very few fish with more than 10 winter rings and therefore, fish assumed to be more than 9 years are grouped together.

Table 2. Mean vertebrae number in the different winter-ring groups in the samples. No. of individuals in brackets.

Sample no.	Number of winter-rings										
	1	2	3	4	5	6	7	8	9	10	>10
1		56.724	57.175	57.105	57.571						56.800
		(29)	(63)	(19)	(7)						(5)
2	55.000	56.520	57.149	56.667	56.714				57.000		
	(5)	(75)	(47)	(9)	(7)				(1)		
3	56.333	56.875	56.977	56.786	56.667	57.000				57.500	
	(3)	(24)	(43)	(14)	(6)	(1)				(2)	
4	56.920	56.722	57.143	56.867	57.174	57.250	57.000	57.000		57.000	57.667
	(25)	(36)	(35)	(15)	(23)	(4)	(1)	(5)		(1)	(3)
5	56.661	56.500	56.808	56.833	57.250		58.000	58.000			
	(59)	(68)	(52)	(6)	(4)		(1)	(1)			
6	56.500	56.933	57.027	57.059	57.333	57.667	56.000	57.167			57.000
	(2)	(15)	(37)	(17)	(33)	(3)	(1)	(6)			(1)
7		56.986	57.246	57.053	57.042	58.000	57.000			56.000	56.000
		(73)	(61)	(19)	(24)	(1)	(1)			(1)	(2)
8		56.877	57.140	56.667	57.667	57.500			58.000		
		(57)	(50)	(6)	(3)	(2)			(1)		
9	56.800	56.286	57.000	57.200	57.000	57.000	56.000				57.000
	(5)	(42)	(57)	(15)	(3)	(1)	(2)				(2)
10	56.333	56.481	56.778	57.023	57.000	57.429	58.000	56.000			57.000
	(6)	(27)	(36)	(43)	(15)	(7)	(1)	(1)			(3)
11	57.000	56.500	56.941	57.115	56.500	57.750		57.000	58.000		56.000
	(1)	(12)	(17)	(26)	(10)	(12)		(1)	(1)		(1)

Fig. 4 shows that only few individuals had more than 5 or 6 winter rings. In sample no. 7 and 8 there were mainly 3 and 4 years old fish, that is individuals belonging to the 1960 and 1961 year-classes.

GROWTH

The samples differed considerably in length frequency distribution (Fig. 5). In samples no. 6 and 11 the 31 cm group was most numerous, and the mean length was above 30 cm (Table 1). The size distribution of the samples no. 7 and 8 differed significantly from the other samples. These two samples consisted entirely of spawning herring, and therefore small herring were not present. The selectivity of the net was supposed to have excluded most of the large herring from the catches.

According to the assumption that the herring in the samples no. 2, 5, 9 and 10 consisted of more races and therefore could have differed in growth rate from the herring in the other samples in the first years, 1_1 and 1_2 were measured in all the samples. The 1_1 and 1_2 frequency distributions are shown in Fig. 6. The 1_1 distributions show no marked difference between the samples, but in the samples no. 2, 5 and 9 there are more small 1_2 values than in the other samples, sample no. 5 showing a bimodal 1_2 curve. The samples no. 2, 5 and 9 had also the lowest mean vertebrae number.

The growth rate, (Fig. 7) for the spawning herring, samples no. 7 and 8, was calculated from scale readings, and so was also the growth

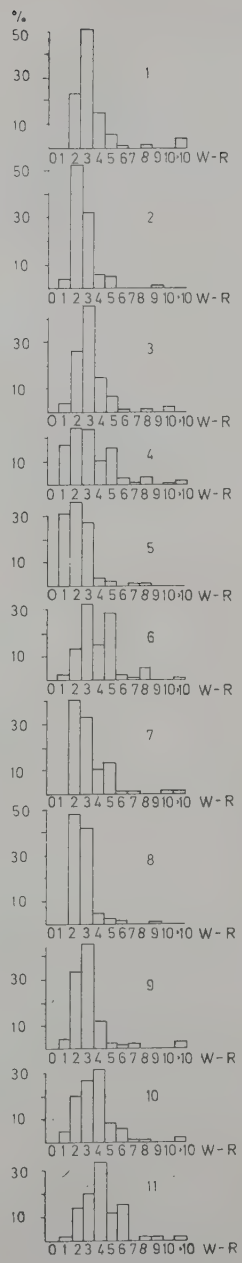


Fig. 4. Age frequency distribution based on the number of winter rings inside the edge. 1) sample no. 1, 25/7—63, 2) sample no. 2, 14/8—63, 3) sample no. 3, 12/9—63, 4) sample no. 4, 17/10—63, 5) sample no. 5, 22/10—63, 6) sample no. 6, 5/11—63, 7) sample no. 7, 27/2—64, 8) sample no. 8, 20/4—64, 9) sample no. 9, 28/7—64, 10) sample no. 10, 25/8—64, 11) sample no. 11, 30/9—64.

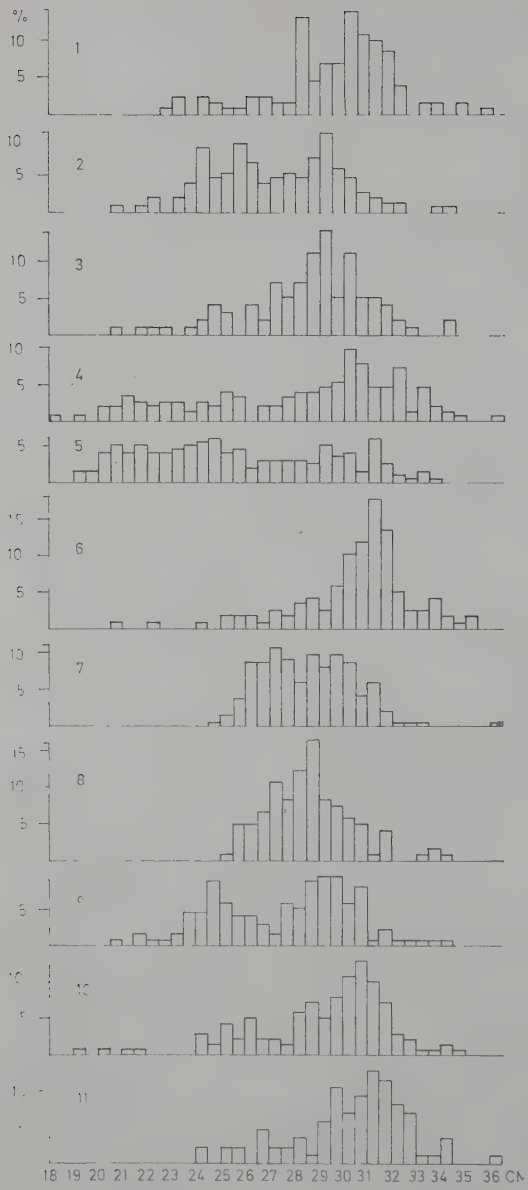
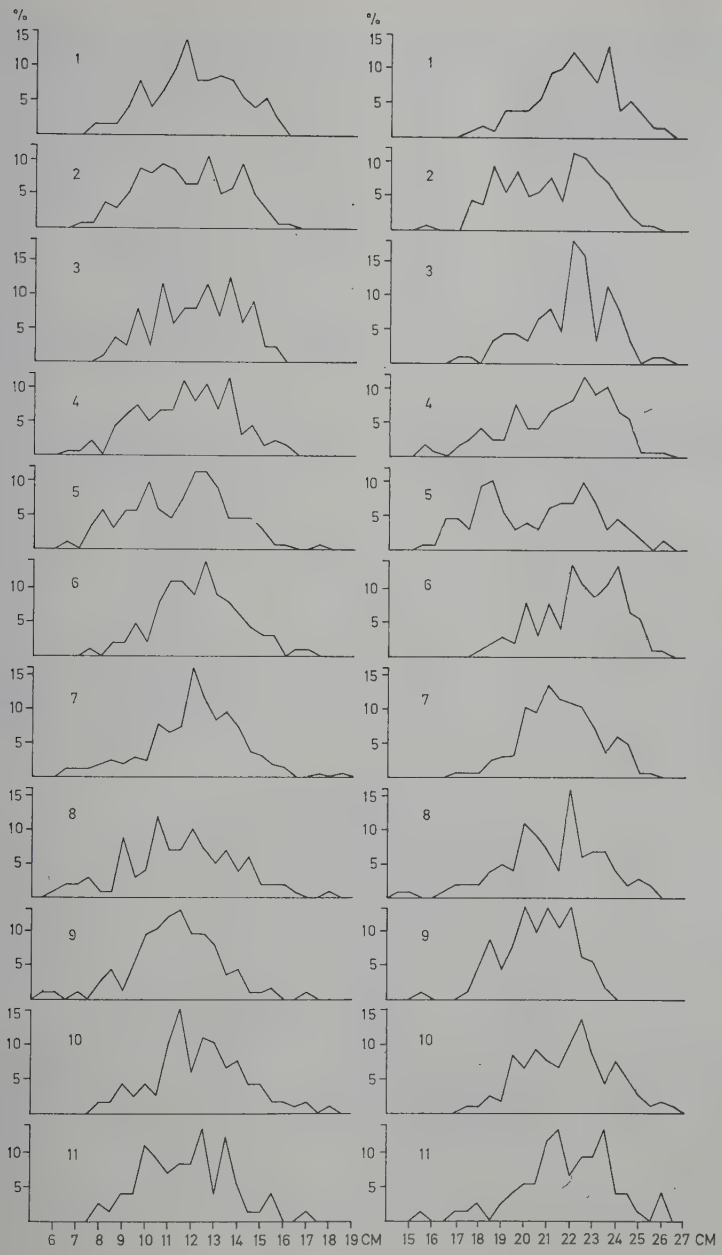


Fig. 5. The length frequency distribution. 1) sample no. 1, 25/7—63, 2) sample no. 2, 14/8—63, 3) sample no. 3, 12/9—63, 4) sample no. 4, 17/10—63, 5) sample no. 5, 22/10—63, 6) sample no. 6, 5/11—63, 7) sample no. 7, 27/2—64, 8) sample no. 8, 20/4—64, 9) sample no. 9, 28/7—64, 10) sample no. 10, 25/8—64, 11) sample no. 11, 30/9—64.

Fig. 6. The frequency distribution of l_1 to the left and l_8 to the right. 1) sample no. 1, 25/7—63, 2) sample no. 2, 14/8—63, 3) sample no. 3, 12/9—63, 4) sample no. 4, 17/10—63, 5) sample no. 5, 22/10—63, 6) sample no. 6, 5/11—63, 7) sample no. 7, 27/2—64, 8) sample no. 8, 20/4—64, 9) sample no. 9, 28/7—64, 10) sample no. 10, 25/8—64, 11) sample no. 11, 30/9—64.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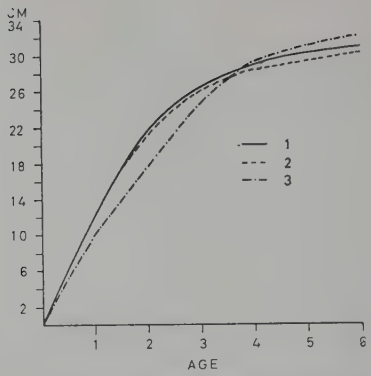

Fig. 7. The growth of the herring. 1) caught with purse seine, samples no. 1, 3, 4, 6 and 11, 2) caught with net, samples no. 7 and 8, 3) Norwegian winter herring, S 2 + 1. from Østvedt (1964).

rate of the herring which were found to belong to one and the same race, sample no. 1, 3, 4, 6 and 11 (Fig. 7). The growth rates were not calculated for herring older than six years as there were too few of them in the samples. There is good conformity between the two growth curves for the first three years. The samples no. 7 and 8 have slightly lower values after the third year. A possible explanation is that the number of the most fastgrowing individuals in these two samples are not representative for the spawning herring due to mesh selection.

SCALE AND OTOLITH CHARACTERS

The size of the central field in scales of the spring spawners may vary considerably. The first winter ring is often very diffuse, and may be difficult to recognize. The other winter rings, however, have more uniform character. Two specimens had scales with the same appearance as scales from the northern type of the Norwegian winter spawning herring. The appearance of the scales in the mixed samples did not differ significantly from the scales of the spring spawners.

The otoliths of spring spawners caught in spawning condition, had an opaque or a small hyaline nucleus (Fig. 8 a and b). The size of the central field varied considerably also in the otoliths (Fig. 8 b and c), but the majority was medium sized. The majority of the otoliths from the samples no. 9, 10 and 11 showed the same characteristics as the otoliths from the samples no. 7 and 8. Some otoliths with one or two winter rings had, however, a large hyaline nucleus and a wide central field (Fig. 8 d and e).

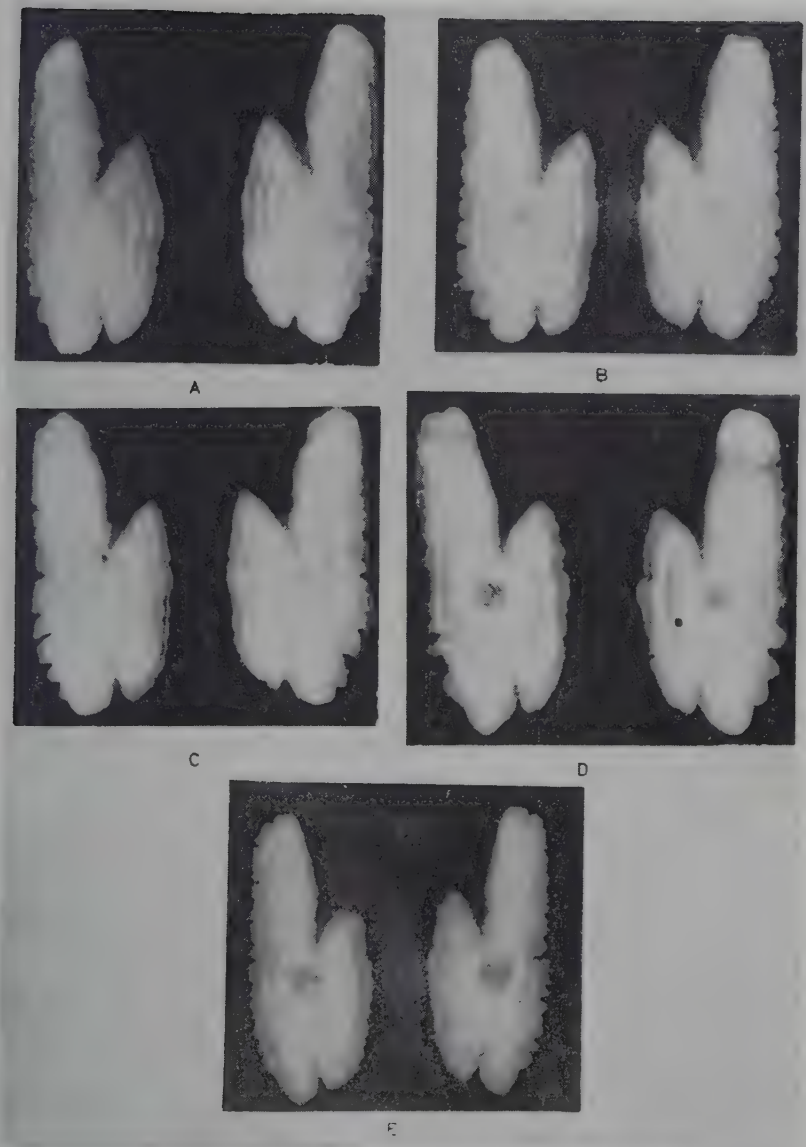

Fig. 8. Different types of otoliths. Further explanation in the text.

Table 3. Maturity stage by month in percent. Sample no. 1 to 6 with four, and sample no. 7 to 11 with eight maturity stages.

1963

Maturity stage	Samples no.					
	1 July	2 Aug.	3 Sept.	4 Oct.	5 Oct.	6 Nov.
I	34.5	63.0	27.7	31.1	58.9	8.0
II	23.1	28.3	60.6	58.2	40.1	91.2
III			7.6	10.8	0.5	0.8
IV						
IV/II	41.5	8.7	4.0		0.5	

1964

Maturity stage	Samples no.				
	7 Febr.	8 Apr.	9 July	10 Aug.	11 Sept.
I			20.6	7.2	8.2
II			18.4	11.5	3.5
III			16.9	30.9	25.9
IV			2.9	24.5	43.5
V	3.8		1.5	5.8	18.8
VI	73.0	84.5			
VII	23.2	14.9			
VIII		0.8	39.7	20.1	

SEXUAL MATURITY AND FAT CONTENT

The maturity stages by month are given in Table 3. The two scales used are not directly comparable, and in trying to get a better impression of the maturity cycle, the «Maturity factor», M_f, was calculated (Aasen 1952). The monthly frequency distribution of the maturity factor is given in Fig. 9. The October distribution contains both samples no. 4 and 5. It appears that M_f increase gradually towards February and April when the samples consisted entirely of spawning herring. In these two samples, M_f varies considerably because some individuals were allready spent.

To get a numeric quantity of the amount of intestinal fat, the fat index, F_i (Wulff 1954), was calculated separatly for each sample. The

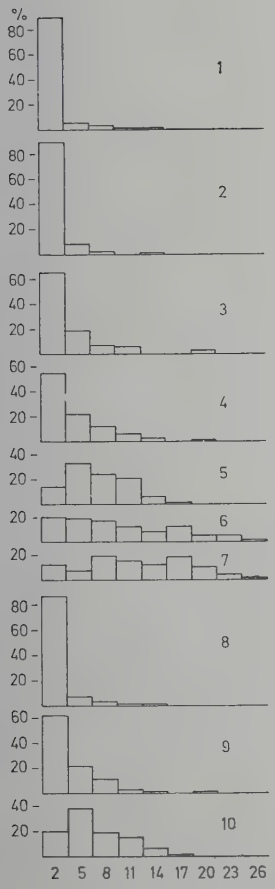

Fig. 9. Monthly variations in the distribution of M_f during the sampling period. 1) July 1963, 2) August 1963, 3) September 1963, 4) October 1963, 5) November 1963, 6) February 1964, 7) April 1964, 8) July 1964, 9) August 1964, 10) September 1964.

fatindex was calculated per 100 individuals, and the values therefore are between 100 and 400. In Fig. 10 are given the monthly mean values of M_f and F_i. The value for October represents the mean of the two samples from that month. The November observation of the fatindex is high compared with the October value, but it should be mentioned that these values are based on subjective examination of the intestinal fat. Where observation are lacking the curves are stippled. The maximum value of M_f is in the period February to April, and the minimum value of F_i is in the same period. The minimum of M_f is in the period just after the spawning with a value of about one. F_i has probably its maximum in July. Observations for June, however, are lacking.

DISCUSSION

The two samples of the spring spawning herring were taken with an interval of two months, and the material indicates that they belong to the same race.

The other samples, which were found to be homogenous, had the same scale and otolith characters as the samples of spawning herring. Neither did the other characters examined show any significant differences between these two groups of samples. It seems likely that all these samples have been drawn from the same population.

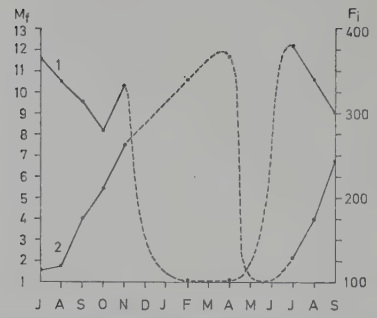

Fig. 10. Cycles of maturity factor and intestinal fat based on monthly mean values. 1) intestinal fat, 2) maturity factor.

As the samples were obtained from different localities along the Telemark coast, the distribution of this population is not limited to a certain fjord. There are no samples in the material from other parts of the Skagerak coast, but observations indicate that this herring population occur not only on the Telemark coast. It is a good correlation in the yearly output (Fig. 1) between the Telemark coast and the Skagerak coast. Spring spawners from the Skagerak coast which were examined by Runnstrøm (1941), had approximately the same high vertebrae number as the herring in the present material. Runnstrøm supposed them to be Kattegat spring spawners or Skagerak spring spawners as they now are named (Andersson 1956). The spring spawners showed also the same characters as the Skagerak spring spawners from Sandefjord examined by Høglund (1964). It is, therefore, reasonable to conclude that the spring spawners in the present material belong to the Skagerak spring spawners.

As mentioned before some of the samples were mixed with young herring with lower vertebrae number, appearently belonging to one or more other races. No spring spawning herring from the adjacent area is known to have such a low mean vertebrae number, and they must therefore belong to autumn spawning races. Previous investigations have demonstrated that autumn spawning herring occur on the Skagerak coast. Broch (1908) found an intermingling of autumn spawners in one of the samples from the Risør district. Runnstrøm (1941) had a strong admixture of the North Sea autumn spawners in samples taken at various parts of the Skagerak coast during the summer and autumn. According to Høglund (1964), one and two years old herring of the

North Sea autumn spawners are always found in varying numbers in the Skagerak area.

ANDERSSON (1958) separates the Kattegat and North Sea autumn spawners on the basis of scale characters, the former having a considerable larger central field than the latter. The Skagerak spring spawning herring have a greater variation in the size of the central field (ANDERSSON 1958). This is confirmed in the present material. It is, therefore, on the basis of the scale characters and the maturity stage of the young herring not possible to separate all the sampled individuals in spring and autumn spawners.

EINARSSON (1951) found in Icelandic waters that the otoliths of the spring spawners had an opaque and the summer spawners a hyaline nucleus. PARRISH and SHARMAN (1958) were able to separate spring and autumn spawners from the North Sea on this character. The same procedure was used for the mixed samples no. 9 and 10. Table 4 shows that the herring with opaque and hyaline nucleus in the otoliths have different vertebrae number. The otoliths with opaque nucleus resemble the otoliths in the present samples containing Skagerak spring spawners. Some of the otoliths with hyaline nucleus (Fig 8 e) resemble otoliths found by PARRISH and SHARMAN (1958) in Buchan herring, and later also in herring from the Bløden Ground, but it could not be concluded whether these autumn spawners belonged to the North Sea or the Kattegat autumn spawners or if it was a mixture of them. It seems, however, possible to separate spring and autumn spawners by otolith characters also on the Norwegian Skagerak coast.

The Skagerak spring spawners in the samples have a fast growth during the first three to four years. Comparing the growth rate with the most fastgrowing type of the 1950 year-class, S 2+1, of the Atlanto-Scandian herring (ØSTVEDT 1964) (Fig. 7) it appears that the Skagerak spring spawners grow faster up to an age of three years, but

Table 4. Mean vertebrae count in the two groups of otoliths in sample no. 9 and 10. a) Otoliths with an opaque or a little hyaline nucleus. b) Otoliths with a hyaline nucleus. Number of individuals in brackets.

Sample no.	a)	b)	% of doubtful cases
9	56.882 (102)	56.409 (22)	6.1
10	56.947 (114)	56.412 (17)	4.3

are then passed by the other. It is not, however, the same year-classes which are compared, but ØSTVEDT (1964) shows that the Atlanto-Scandian herring have had an increased growth rate and that the most marked increase was in the period from 1951 to 1963. The difference in growth rate between the two races in the first years, therefore, is probably not of the size shown in Fig. 7.

In accordance with the findings of HØGLUND (1964) the 1960 year-class dominates the present homogenous samples both in 1963 and 1964, except sample no. 4 and the two samples with spawning herring. The age frequency distribution of the spawning herring seems to show that a great part of the Skagerak spring spawners are first time spawners at an age of three years. This is earlier than for the southern type of the Atlanto-Scandian herring which ØSTVEDT (1958) over a long period of years found to be first time spawners at a nearly constant mean age of about 4.4 years.

The maturity and the intestinal fat cycles were inversed, with a quicker building up of the intestinal fat than the breaking down, and opposite with the maturity factor as found by AASEN (1952). The maturity factor showed a maximum in February to April and a minimum in May — June, while the intestinal fat had a maximum in July, and thereafter gradually decreased to a minimum in the winter months as also observed by AASEN (1952) for the spring spawning herring in Lusterfjord.

SUMMARY

1) The material was collected on a little part of the Norwegian Skagerak coast in 1963—1964.
2) The following data were sampled: total length and weight, stage and weight of gonads, intestinal fat content, vertebrae number and scales. Otoliths were taken from the last 5 samples.
3) Most of the herring examined appeared to be Skagerak spring spawners with a mean vertebrae number of about 57. Some of the herring with one and two winter rings were autumn spawners, belonging to either the North Sea autumn spawners or the Kattegat autumn spawners.
4) The otoliths of the Skagerak spring spawners had an opaque or a little hyaline nucleus with varying size of the central field. Some of the otoliths in the autumn spawners resemble otoliths previously found in the North Sea.

5) The Skagerak spring spawners had a rapid growth the first three years, and were spawning for the first time at three years age.
6) The maturity and the intestinal fat cycles appeared to be inversed.

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STUDIES ON SERUM ESTERASE IN HERRING AND SPRAT

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INTRODUCTION

Serology and molecular biology have been used in segregation studies of herring, *Clupea harengus* L., on several occasions. Sindermann and Mairs (1959) found two herring populations in the Gulf of Main by frequencies of erythrocyte antigenes. They also found variability in serum protein patterns. Some variations were found to be connected with diseases, some were probably related to age, but some offered hope of electrophoretic characterization of the populations (Sindermann and Mairs 1958, Mairs and Sindermann 1960). Sindermann and Honey (1963) did not find intraspecific variations in electrophoretic mobility of herring hemoglobins, and Wilkins and Iles (1965) found hemoglobin types related to body length. Transferrin types were described by Nævdal and Haraldsvik (1966), and Odense, Allen and Leung (1966) applied types of the enzymes lactate dehydrogenase and aspartate aminotransferrase in studies on Canadian herring populations.

In the present paper intraspecific variations in herring esterase phenotypes are described, and an attempt is made to reveal the genetic basis of the variations. Intraspecific variations in esterase phenotypes of sprat, *Sprattus sprattus* (L.), are also studied.

Part of the results concerning herring have been presented in a preliminary report (Nævdal and Danielsen 1967).

MATERIAL AND METHODS

Blood was sampled by cardiac puncture or by cutting the tail. The samples were sent on ice in thermo bottles to the laboratory where they were centrifuged. Most sera were analysed fresh, but some samples had to be stored deep frozen for some weeks before the analyses could be carried out.

The sera were analysed by combined starch and agar gel electrophoresis (Sick 1965, Møller 1966) for 75 minutes. For identification of

the esterase components, the gels were immersed in a freshly prepared solution containing 4 ml 1% solution of 1-naphtyl acetate in acetone and 200 mg Fast Blue Salt BB in 100 ml of destilled water. The bands of esterase activity were then developed within few minutes.

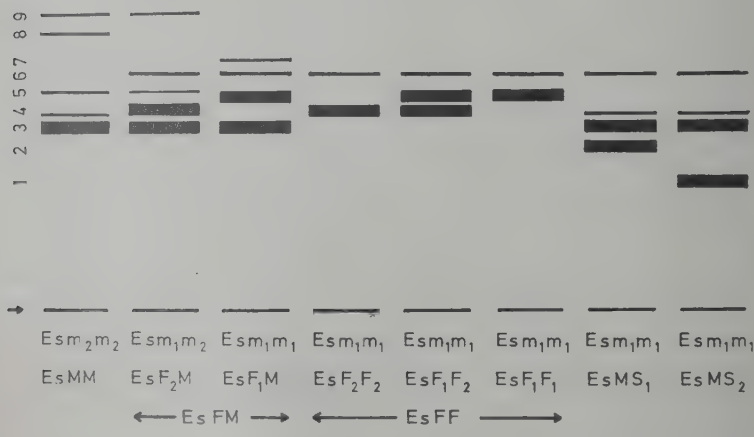
Sampling localities, numbers in samples and date of sampling are listed in Table 1 (herring) and Table 2 (sprat).

RESULTS AND DISCUSSION

HERRING

The esterase molecules moved towards the anode. One or two strong and up to six weak esterase bands were found. The electrophoretograms are outlined in Fig. 1.

In most specimens only one strong esterase band was present. This band and the corresponding esterase molecular type was named Es M (middle). Two bands of higher anodic mobility than Es M occurred


1 2 3 4 5 6 7 8 9
Esm$_2$m$_2$ Esm$_1$m$_2$ Esm$_1$m$_1$ Esm$_1$m$_1$ Esm$_1$m$_1$ Esm$_1$m$_1$ Esm$_1$m$_1$ Esm$_1$m$_1$
EsMM EsF$_2$M EsF$_1$M EsF$_2$F$_2$ EsF$_1$F$_2$ EsF$_1$F$_1$ EsMS$_1$ EsMS$_2$
Es FM
Es FF

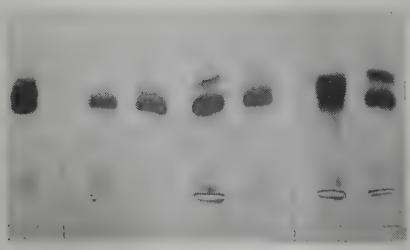


Fig. 1. Outline of serum esterase phenotypes in herring by combined starch and agar gel electrophoresis at pH 9.0, together with a photograph of patterns obtained by routine analyses. Legend: Filled in bars: Strong bands. Single lines: Weak bands. Arrow indicate the point of application.
1: Es S_2, 2: Es S_1, 3: Es M, 4: Es s(weak) and Es F_2(strong), 5: Es m_2 (weak) and Es F_1(strong), 6: Es m_1, 7: Es f_3, 8: Es f_2, 9: Es f_1.

Sample no.	Locality and date of sampling	Indications of sample		Types of weak esterase zones					Types of strong esterase zones								
				Es m_1 m_1	Es m_1 m_2	Es m_2 m_2	No.	q_1	Es FF	Es FM	Es MM	Es MS_1	Es MS_2	No.	q_F	q_{S_1}	q_{S_2}
1.	Austfjorden, Hordal. 30 March—15 May 1967	Spring spawners in spawning condition	obs.	30	49	7	86	0.63	—	4	93	—	—	97	0.02	—	—
			exp.	34	40.1	11.8			0.04	3.8	93.2	—	—			—	—
2.	61°10' N, 06°00' E North Sea May 1967	Mainly immatured autumn spawners	obs.	91	21	1	113	0.90	—	7	131	—	—	138	0.03	—	—
			exp.	91.5	20.3	1.1			0.1	8.0	129.8	—	—				
3.	Masfjorden, Hordal. 12 June 1967	Immatured	obs.	67	16	3	86	0.87	1	5	89	2	—	97	0.04	0.01	—
			exp.	65.0	19.5	1.5			0.2	7.4	87.5	1.8	—				
4.	61°10' N, 00° 35' W, North Sea 17 June 1967	Adult autumn spawners	obs.	43	1	—	44	0.99	—	2	47	—	—	49	0.02	—	—
			exp.	43.1	0.9	0.0			0.02	1.9	47.1	—	—				
5.	61°10' N, 00°35' W, North Sea 17 June 1967	Adult spring spawners	obs.	47	—	—	47	1.00	—	3	46	—	1	50	0.03	—	0.01
			exp.	47.0	—	—			0.05	2.9	46.1	—	1.0				
6.	58°11' N, 03°48' E, North Sea 1 July 1967	Adult autumn spawners	obs.	87	3	—	90	0.98	—	1	96	—	—	97	0.05		—
			exp.	86.4	3.5	0.0			0.0	1.0	96.0						
7.	55°00' N, 06°00' E, North Sea 24/25 Aug. 1967	Adult autumn spawners	obs.	78	30	1	109	0.85	—	6	112	—	—	118	0.03	—	—
			exp.	78.8	27.8	2.5			0.1	6.9	111.0	—	—				
8.	Tistam, Nordfjord 14 Oct. 1967	0-gr.	obs.	79	3	—	82	0.98	—	13	85	—	—	98	0.07	—	—
			exp.	78.8	3.2	0.04			0.5	12.8	84.8	—	—				
9.	Borgenfj., Trøndelag 26 Oct. 1967	0-gr.	obs.	98	5	—	103	0.98	—	7	95	1	—	103	0.03	0.005	—
			exp.	98.9	4.0	0.04			0.1	6.0	95.9	1.0	—				
10.	57°35' N, 10°55' E, Kattegat 8 Nov. 1967	1-gr., autumn spawners	obs.	68	8	1	77	0.94	3	7	76	—	—	86	0.08	—	—
			exp.	68.0	8.7	0.3			0.6	12.7	72.8	—	—				

in some specimens. These components, named Es F_1 (fast) and Es F_2, were in most cases found together with Es M. In only one specimen Es F_1 and Es F_2 occurred together. Distinction between Es F_1 and Es F_2 was difficult in routine analyses, and therefore they were lumped together and named Es F. Two bands, named Es S_1 (slow) and Es S_2, of anodic mobility lower than Es M also occurred at low frequencies, and always in combination with Es M. The mobility of Es S_2 differed greatly from the mobility of Es M, while the mobilities of Es M and Es S_1 were little different.

The phenotype with only the Es M component was named Es MM, and the other phenotypes were named according to the components they contained, i.e. Es FM, Es FF, Es MS_1 and Es MS_2 (Fig. 1).

The three weak bands of greatest anodic mobility were supposed to belong to one group of esterase molecules and designed Es f_1, Es f_2 and Es f_3. The two weak bands of intermediate mobility were designed Es m_1 and Es m_2. Additional bands occurred near Es m_1 and Es m_2 in some specimens, but they could not be effectively separated from them by the present method, and therefore they have been omitted in the following discussion.

The slowest moving weak band, named Es s, (and partly also Es m_2) were screened by the stronger Es F bands when one of the latter was present. The relative mobilities of the various bands are shown in Fig. 1. Especially the Es f_1 and Es f_2 bands varied considerably in strength, and occasionally they were nearly as strong as the Es M component.

The phenotypes of the strong components could be determined from sera which had been frozen, but the patterns were clearer when fresh sera were used. The weak components, however, often were too diffuse to be determined from frozen sera.

The strong components may be explained as the product of separate genes (possibly allelic) named Es^F, Es^M, Es^{S_1}, and Es^{S_2} (where indices indicate the components which the genes are supposed to control). The hypothetical homozygotes Es S_1S_1 and Es S_2S_2 and the heterozygotes Es FS_1 and Es FS_2 were not found, but it appears from the distributions of phenotypes in Table 1 that the genes Es^F Es^{S_1} and Es^{S_2} were so rare that the lacking combinations should not be expected in the present samples. Except for sample 10 the population data are in fairly good accordance with expected Hardy-Weinberg distributions, and this supports the introduced hypothesis. Sample 10, however, show a surplus of hypothetical homozygotes and therefore to some extent contradict the hypothesis. If this sample is drawn from a panmixed population, the result indicates alternative explanations of the variations (genetic or non genetic).

If the variations in the weak components are genetically controlled, several gene loci must be involved, or the variations must be caused by formation of stable polymeres. For use in segregation studies of herring populations, the components Es m_1 and Es m_2 may have some importance. One or both of these occurred in nearly all specimens. When they were absent, it was always in specimens with weak total consentration of esterase or with low enzymatic activity in the sera. Three phenotypes occurred, and they were called Es m_1m_1, Es m_1m_2, and Es m_2m_2. Two allelomorphic genes, called Es^{m_1} and Es^{m_2}, were assumed to control these phenotypes. In Table 1 are listed the observed distributions of the m_1m_2-phenotypes and the calculated frequencies of the hypothetical gene Es^{m_1}. The numbers of specimens classified as m_1m_2-types were lower than the numbers classified as types of strong components, because the m_1m_2-bands in some specimens were too weak for reliable classification. When observed distributions of phenotypes were compared to expected distributions of genotypes according to the Hardy-Weinberg law, fairly good accordance was found (Table 1,) and except for sample 1 the deviations were not significant when tested by common χ^2-tests. Sample 1 gave a significant excess of hypothetical heterozygotes, and therefore contradict the hypothesis. However, the good accordance between expected and observed distributions in the other samples supports the hypothesis.

Breeding experiments have been planned to test the hypothesis of genetical control of the esterase phenotypes in herring.

There was no evidence of dependence on factors other than genetic of the variations of esterase phenotypes. The variations occurred in all age groups and in both sexes. However, it should be emphasized that the present analyses were only qualitative, and that variations in strength of esterase activity may occur which were not recorded by the present method.

Table 1 shows that there was no great variations among samples in distributions of strong esterase phenotypes. Es S_1 and Es S_2 were only found at very low frequencies in two and one sample respectively, but this did not show significant differences from the rest of the samples. The Es F bands occurred at low frequencies in most samples, but in samples 8 and 10 their hypothetical controlling gene was found at a frequency of 0.07 and 0.08 respectively, indicating real differences among the populations from which the samples were drawn.

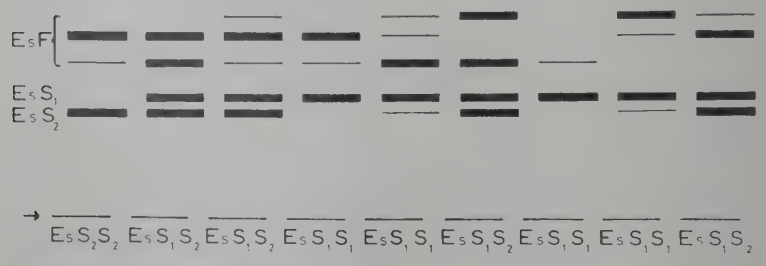
The distributions of the Es m types varied considerably, and although Es m_1m_1 occurred at high frequencies in most samples, it was found at lower frequencies in spring spawners from the coast (samples 1 and 3) and in one sample of autumn spawners from the North Sea (Sample 7).

SPRAT

Very extensive and complicated variations in serum esterase were revealed in sprat by combined starch and agar gel electrophoresis, and several patterns were found (Fig. 2). The patterns comprise variation in at least five zones of weak esterase activity. The three fastest moving components were supposed to belong to one group of esterase components and called Es F (fast) while the two slower moving were called Es S

Table 2. Observed distributions of esterase phenotypes in one year old sprat compared with expected distribution according to the Hardy-Weinberg law.

Sample no., locality and date of sampling		Esterase phenotypes			No.	q_1
		EsS_1S_1	EsS_1S_2	EsS_2S_2		
1. Kattøya, Langesund-fjorden	obs	15	35	33	83	0.39
3 Oct. 1966	exp	12.6	39.5	30.9		
2. Nå, Hardangerfjorden	obs	19	38	30	87	0.44
14 Oct. 1966	exp	16.8	42.9	27.3		
3. Risnes, Masfjorden	obs	10	44	30	84	0.38
4 June 1961	exp	12.1	39.6	32.3		
4. Skorpo, Hardangerfjorden.	obs	29	31	8	68	0.65
6 June 1967	exp	28.7	30.9	8.3		
5. Gjermundshamn, Hardangerfjorden	obs	22	21	6	49	0.66
6 June 1967	exp	21.3	22.0	5.7		



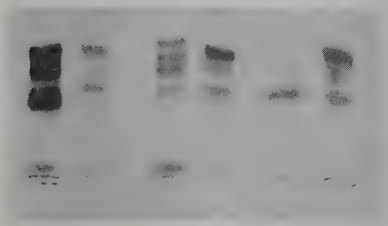


Fig. 2. Outline of serum esterase phenotypes in sprat by combined starch and agar gel electrophoresis at pH 9.0, together with a photograph of patterns obtained by routine analyses. Legend: Fig. 1.

(slow). A considerable part of the specimens showed diffuse electrophoretograms, and only the two slowest moving components, named Es S_1 and Es S_2 (which sometimes appeared double), were clear enough to form the basis for classification. One or both of these components were present in all specimens. When not taking into account the weak bands which often were present at position of lacking strong bands (Fig. 2), the specimens could be classified into three phenotypes on basis of the variations in Es S_1 and Es S_2 bands. These phenotypes were called Es S_1S_1, Es S_1S_2, and Es S_2S_2 according to which of the bands they posessed. The distributions of the phenotypes in five samples are shown in Table 2.

When a hypothesis of genetical control involving two allellomorphic genes, named Es^{S_1} and Es^{S_2}, is introduced, it appears that there are fairly good accordance between observed distributions of phenotypes and expected distributions of genotypes (Table 2). The hypothesis may accordingly explain the present variation in the zones Es S_1 and Es S_2. However, the variations in the other zones are still unexplained, and it is impossible to have any idea of the control of these variations as long as the specimens can not be classified with a reasonable degree of reliability.

It appears from Table 2 that there were considerable differences among samples in distributions of the phenotypes, and thus in frequencies of the hypothetical genes. Although the type determinations may be somewhat unreliable, the variations among samples were greater than may be explained by incorrect type determination or by errors of sampling. Thus the differences probably represent real differences between the populations from which the samples were drawn. This coincides with results from analyses of hemoglobins and transferrins (Nævdal 1968 and unpublished) which show significant frequency variations among samples of sprat from Norwegian waters. But because the type determination are somewhat unprecise, variations in esterase patterns in sprat appear at present to be of little value in segregation studies.

SUMMARY

1. Herring and sprat serum esterase has been studied by combined starch and agar gel electrophoresis at pH 9.0. Both strong and weak bands which represented esterase activity occurred in both species.
2. Most herring specimens contained one strong component of intermediate anodic mobility. Two strong components of higher and two of lower anodic mobility occurred at low frequencies. A hypothesis of genetical control by one gene controlling each of the components is proposed.

3. Maximum six weak bands of herring serum esterase were found. Considerable variations among specimens occurred in these bands. No theory of genetic control of the total variations can be given at present, but two codominant alleles may be responsible for the variation in two of the weak bands.
4. The intraspecific variations in sprat serum esterase were complicated, and it was difficult to classify the specimens into well defined groups on basis of these variations. A hypothesis of control by two allelic genes of the variations in two of the components is introduced.
5. Frequency variations among some of the samples of both species were indicated.

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STUDIES ON HEMOGLOBINS OF SOME GADOID FISHES

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INTRODUCTION

During the last few years it has been shown that in fish hemoglobins there excist intraspecific variations of at least two types, namely ontogenetic as in salmon (Kock, Evans, and Bergstrøm 1964, Vanstone, Roberts, and Tsuyuki 1964) and herring (Wilkins and Iles 1966), and genetically controlled polymorphism as first found in whiting and cod (Sick 1961). In sprat (Wilkins and Iles 1966, Nævdal 1968) and some other clupeoid fishes (Simpson and Simon Schlothfeldt 1966) intraspecific hemoglobin variations have been described, but these variations were neither found to be assosiated with age or length, nor has the genetic basis of the variations been worked out completely.

The present work is part of a search program to find polymorphic characteristics for use in segregation studies of fish populations. Most interest have been paid to gadoid fishes of commercial value, but bloods of minor economic important species have also been analysed for comparison.

MATERIAL AND METHODS

Blood samples have been obtained by cardiac puncture. Heparin or citrate was used as anticoagulant. The blood specimens were stored cold (0—4°C), and analyses were carried out within a few days after sampling.

Agar gel electrophoresis, described by (Sick 1965) was applied. Each run lasted for 60 minutes with about 50 volts between ends of gel. To control the results obtained by this method, part of the material was also analysed by combined starch and agar gel electrophoresis (Møller 1966) with 65 volts between ends of gel for 90 minutes.

Blood samples were collected from gadoid fishes from localities along the Norwegian coast and in the North Sea. Species, localities, date of

sampling and numbers are listed in Table 1 where the results also are presented. Scientific names and the order of the species are after Svetovidov (1962).

RESULTS AND DISCUSSION

The hemoglobin components of all the species concerned here, moved towards the cathode in agar gel at pH 7.3. Fig. 1 shows the relative mobilities of the hemoglobin components and the hemoglobin pattern found for each species except forked hake. For comparison the cod hemoglobin type HbI–1–2 is shown. The hemoglobin of the forked hake moved only insignificantly by this method.

In all species, except forked hake, one or two strong and at least two weak or moderately strong components were observed. The electrophoretic mobility of the strong components did not differ very much from the mobility of the strong hemoglobin components of cod. The highest cathodic mobility of strong components was found in coalfish, the lowest in blue ling. The mobilities of the strong components of the other species were found within this range.

Intraspecific variation occurred in most species. In the following the same designations are used for corresponding patterns (phenotypes) of different species, although the mobilities of the components were not identical (Fig. 1).

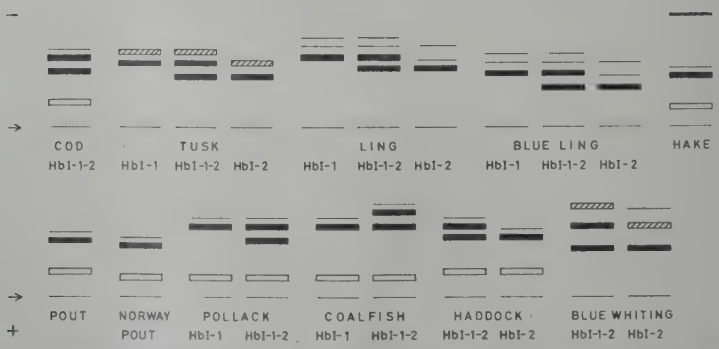

Fig. 1. Hemoglobin patterns of gadoid fishes obtained by agar-gel electrophoresis at pH 7.2. Filled in bars) strong bands, open bars) Hb II-components [moderately strong bands], cross hatched bars) other moderately strong bands, single lines) weak bands. Arrows indicate the points of application.

In tusk, ling and blue ling hemoglobin patterns with either one or both of two strong hemoglobin components were found. These patterns were similar to the hemoglobin patterns of whiting and cod (Sick 1961), and a similar nomenclature was chosen. Thus the components were named HbI-1 and HbI-2 in order of decreasing cathodic mobility, and the hemoglobin types were called HbI-1, HbI-1-2, and HbI-2, according to which of the components they possessed.

No evidence of ontogenetic variation in the hemoglobin of these species was found. The variations may be explained, however, by assuming that two allelomorphic genes, named *HbI*[1] and *HbI*[2], control the synthesis of the components HbI-1 and HbI-2 respectively. This corresponds to the genetical control of whiting and cod hemoglobin types (Sick 1961). The accordance between observed distributions of hemoglobin types (phenotypes) and calculated Hardy-Weinberg distribution of genotypes greatly supports this hypothesis (Table 1).

Two strong hemoglobin components, named HbI-1 and HbI-2, also occurred in pollack, coalfish, haddock and blue whiting, but only one of the single banded phenotypes was found in each species. However, the distribution and the calculated gene frequencies show that one of the hypothetical genes is too rare to be expected in a homozygotous state in the present material (Table 1). Therefore a corresponding mode of inheritance of hemoglobin types may exist also in these species.

In coalfish variations were very rare as only one specimen of 288 differed from the normal hemoglobin pattern of this species. In hake, pout and Norway pout no individual variations in the strong hemoglobin components were found.

In all species the strong components were accompanied on their cathodic side by weaker components named HbI-1' and HbI-2'. Sick (1961) found that corresponding components in whiting and cod increased in strength upon storing. This was evidently also the case in the species concerned here.

In ling and blue ling other weak components, named HbI-1'' and HbI-2'', of still higher cathodic mobility were present (Fig. 1). Also these components varied among specimens, but they often had a rather diffuse appearance, and therefore further studies have not been undertaken. In hake a moderately strong component with about twice as great cathodic mobility as the major hemoglobin component, was present in some of the specimens.

Components similar to the HbII components of whiting and cod (Sick 1961) were found in hake, pout, Norway pout, pollack, coalfish and haddock at positions between the point of application and the major components. The relative mobilities of these components differed among

species, and also intraspecific variations were indicated although not clear enough for classification of specimens into well defined groups. Except for some very faint bands, no components comparable to HbII components could be detected in tusk, ling, blue ling and blue whiting.

The intraspecific variations described here could also be found by combined starch and agar gel electrophoresis at pH. 9.0 (anodal movement). This confirms that the variations are real molecular differences and not methodical artifacts. By this method also the hemoglobins of forked hake moved towards the anode, but no intraspecific variation were found in this species.

Although the material was limited, the present observations clearly showed that intraspecific variations of the hemoglobin molecules, probably genetically controlled, are present in several gadoid species.

The different distribution of the hemoglobin types in the samples of ling (Table 1) indicate that different random mating populations excist in this species. However, the numbers of specimens are too low for reliable deductions.

The studies of protein polymorphism in fishes are increasing. Although yet insufficient to give a total survey, and despite different methods and lack of common reference, polymorph systems of one protein type often seem to be characteristic for one taxonomic group (family etc.), while systems of another protein are characteristc for others, for instance polymorphism in hemoglobins for *Gadidae* (Sick 1961) and in esterase for *Scombridae* (Sprague 1967, Nævdal unpublished.).

SUMMARY

1. Hemoglobin of tusk, forked hake, ling, blue ling, hake, pout, Norway pout, pollach, coalfish, haddock and blue whiting were studied by agargel electrophoresis.
2. Both inter- and intraspecific variations in hemoglobin patterns occurred.
3. Intraspecific variations were found in tusk, ling, blue ling, pollack, coalfish (only one specimen differed from the «normal» pattern), haddock and blue whiting.
4. A hypothesis of genetical control involving two allelomorphic genes is proposed to explain the variations within each species. The population data coincided with this hypothesis.
5. No indication of ontogenetic variation of hemoglobin patterns have been found.
6. Frequncy variations of the hemoglobin types in ling indicate segregetion in the population structure.

Table 1. Material analysed for hemoglobin polymorphism. Observed distributions of types compared with the expected distributions of genotypes according to Hardy-Weinberg law.

Species, locality, and date of sampling	Distribution of hemoglobin types						No.	Frequency of the *HbI*^{1} allele
	HbI–1		HbI–1–2		HbI–2			
	obs.	exp.	obs.	exp.	obs.	exp.		
Tusk, *Brosme brosme* (Müll.)								
N. 60°20', E. 4°20' ..... 24/ 5—67	5		9		4		18	
N. 62°56', E. 6°07' ..... 6/ 9—67	1		4		2		7	
N. 61°52', E. 1°23' ..... 8/ 9—67	6		19		8		33	
Total	12	13.4	32	28.9	14	15.7	58	0.48
Forked hake, *Phycis blennoides* (Brünn.)								
N. 61°52', E. 1°23' ..... 8/ 9—67			monomorphic				38	
Ling, *Molva molva* (L).								
Tennholmen, Nordland ..... 6/10—66	—		3		4		7	
Myking, Hordaland ..... 4—67	—		5		9		14	
N. 61°52', E. 1°23' ..... 8/ 9—67	1		7		9		17	
Total	1	1.8	15	13.0	22	23.1	38	0.22
N. 60°51', E. 3°02' ..... 27/ 2—68	—		1		56		57	0.08
Blue ling, *M. dipterygia* (Penn.)								
N. 60°20', E. 4°20' ..... 24/ 5—67	1	1.0	12	12.3	38	37.7	51	0.14
N. 61°52', E. 1°23' ..... 8/ 9—67	2	1.7	24	24.3	89	89.1	115	0.12
Hake, *Merluccius merluccius* (L).								
N. 60°20', E. 4°20' ..... 24/ 5—67			monomorphic				15	
N. 61°52', E. 1°23' ..... 8/ 9—67			monomorphic				37	
N. 60°51', E. 3°02' ..... 27/ 2—68			monomorphic				9	

Pout, *Trisopterus luscus* (L).									
N. 53°35', E. 2°56'	16/ 9—67			monomorphic				27	
Norway pout, *T. esmarkii* (Nilss.)									
N. 62°56', E. 6°07'	6/ 9—67			monomorphic				50	
Pollach, *Pollachius pollachius* (L.)									
Myking, Hordaland	4—67	76	76.2	5	4.7	—	0.01	81	0.97
Coalfish, *P. virens* (L.)									
Hordaland	16/12—65	—		—		114		114	
Veidholmen, Nordmøre	17/12—65	—		1		33		34	
Røstbanken, Lofoten	9/ 3—66	—		—		140		140	
Total		—		1		287		288	0.002
Haddock, *Melanogrammus eglefinus* (L.)									
Hjelmsøy, Finnmark	28/ 5—65	—		1		115		116	
Malangen, Troms	28/10—65	—		1		97		98	
Total, Northern Norway		—		2		212		214	0.004
Myking, Hordaland	4—67	—	0.1	5	4.9	80	80.0	85	0.03
Blue whiting, *Micromesistius poutassou* (Risso)									
N. 60°20', E. 4°20'	24/ 5—67	—		—		50		50	
N. 59°15', E. 3°35'	19/ 8—67	—		—		87		87	
N. 57°32', E. 7°57'	22/ 8—67	—	0.1	4	4,3	70	69.9	74	0.03
N. 62°56', E. 6°07'	6/ 9—67	—		—		91		91	

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CONTRIBUTIONS
GIVEN IN HONOUR OF

GUNNAR ROLLEFSEN

AT HIS 70TH BIRTHDAY

EDITORS:
ERLING BRATBERG ERLING BAKKEN
ODD NAKKEN

Günnar Rollefsen

FiskDir. Skr. Ser. HavUnders., *15*: 103–107.

FOREWORD

Gunnar Rollefsen was born November 20, 1899. His parents were factory owner, later bank manager, Hans Georg Rollefsen and Anna Marie, n. Christensen. The family lived in Larvik, a town by the Oslofjord, and here Gunnar Rollefsen finished his pre-university education in 1920. His boyhood interest in living organisms of all kinds led him on to a study of zoology at the University of Oslo.

In 1927, before Rollefsen had completed his university studies, he was offered a fellowship to take up research at the scientific department of the Directorate of Fisheries in Bergen. At that time he was working on his thesis on freshwater fish. In Bergen, however, Rollefsen started investigations on marine plankton, and soon concentrated on fish eggs, especially eggs of cod. From simple, discarded parts of mechanical equipment he succeeded in making an apparatus that automatically at short intervals photographed the development of cod and flounder eggs. This made it possible to describe in detail the hatching process under various conditions. During this period he also studied the effect of mechanical influences on the cod egg, and demonstrated that the action of waves and breakers are responsible for a heavy mortality among the eggs.

During his first years in Bergen Rollefsen took part in many cruises, and enjoyed the work aboard the first ship named "Johan Hjort". This was a small cutter able to operate in inshore or nearshore waters only.

The scientific staff was small and Rollefsen undertook investigations in biology as well as physical oceanography. Rollefsen's principal interest, however, was in studies of the cod in Lofoten. He worked on the age determination of this fish and found that the otoliths gave a more reliable indication of age than the scales. In addition he discovered that the two subpopulations, the coastal cod and the "skrei", could be separated by their otolith patterns, and he was furthermore able to distinguish the zones in the otoliths representing the years of spawning. The details in the life history of each cod, as revealed from the otoliths, formed the basis for a series of prognoses on the strength of the year-classes and the prospects for the cod fishery.

Supported by grants from research funds established by the fishing industry, Rollefsen initiated a new approach to a major problem in fisheries: what causes the great fluctuations in year class strength in fish stocks? And further: is it possible to diminish these fluctuations by artificial hatching and rearing? In 1934 experiments were started in Trondheim to rear a hybrid between two species of flounders. The hybrid is very rare in nature, but ecologically fully competitive and easy to recognize. Millions of these "marked" fry were released in an enclosed fjord and their further destiny closely watched. The hybrid turned out to be superior compared to the natural flounders. However, some estimates of mortality could be made, and a lot of practical experience on artificial propagation on fish was collected. In particular, the problem of finding suitable food for the larvae was solved. Unfortunately, the experiments had to be discontinued when World War II broke out.

During the war it was impossible to carry out usual field work, and investigations had to be concentrated on providing samples from the greater seasonal fisheries, mainly cod and herring. An unbroken series of observations on the age composition in these stocks was therefore maintained.

A great interest in applied research had developed when war ended in 1945. Rollefsen realized this, and he started to work hard on obtaining what he regarded as a major requirement for further studies: an ocean-going research vessel. Despite the fact that a shortage of steel, engines and equipment existed, his persistent argumentation resulted in the go-ahead from the Government. The ship was built from a hull intended for a whaler and completed as "G. O. Sars" in 1950.

The design of the 170-foot ship proved very successful for all the varied purposes for which she was needed. Her general layout was copied when the new "Johan Hjort" was built 8 years later. But this time the need for a new research vessel was advocated strongly by the fishermen's organizations as well.

Rollefsen was appointed director of the Institute of Marine Research in 1947 after acting as head for some years. As director he had to devote an increasing part of his work to planning and administration. The staff increased from 25 persons to more than 100 under Rollefsen's leadership, and many new research projects were taken up. Not only was the biology of commercially important marine species studied, but investigations of the physical and chemical environment, the biochemistry and physiology of fishes, applications of hydroacoustics, and studies of invertebrates became increasingly important.

Besides his work at the Institute Rollefsen played a prominent part in international organizations. He attended the meetings of the International Commission for the Exploration of the Sea (ICES) for the first

time in 1934. Later he met regularly in several of the ICES' committees and became chairman of the Northeastern Area Committee in 1945 and of the Gadoid Fish Committee in 1954, an office he filled until 1958. He was elected Vice President in 1957 and First Vice President a year later. Rollefsen took an active part in the meetings, and as chairman he arranged several group meetings of expert biologists on specially important topics. He realized that ICES would benefit greatly if organized as a completely independent international body. In cooperation with other members of the Bureau he contributed to an agreement with the Danish Government and a Convention for ICES in order to clarify the status of the body.

Rollefsen's contribution to international cooperation among scientists and fisheries administrators was not limited to ICES, but included international fisheries commissions as well. He took part when the International Commission for the Northwest Atlantic Fisheries (ICNAF) was established in Washington D. C. in 1949, and attended all annual meetings of that commission as a delegate until 1961. Within ICNAF he always emphasized the importance of a rational management of the resources, but at the same time put the case for the Norwegian fisheries when needed.

On the east side of the Atlantic, especially the North Sea, management of the marine fisheries was organized internationally under the Permanent Commission of the International Fisheries Convention of 1946. On the Commission Rollefsen met as a delegate from the time the organization was established until it was reorganized as the North East Atlantic Fisheries Commission in 1958, and he was the Vice President between 1953 and 1956. His work here was mainly related to studies of the effect of mesh sizes and of size limits of fish, and he was the chairman of a committee established to report on these problems.

The trawler fleets of all nations increased greatly after World War II. It was felt by many that their exploitation of the fish stocks on the banks along the Norwegian coast was a threat to the livelihood of the Norwegian fishermen who traditionally depended on these resources and mainly used gillnets and longlines.

Rollefsen's view was that the Norwegians ought to develop a trawler fleet of their own, but apart from this, needed protection of the nearshore waters. He therefore gave very valuable assistance at the International Court of Justice in the Fisheries Case between United Kingdom and Norway in 1951 where the Norwegian base lines determining the fishery limit fixed by the Royal Norwegian Decree of July 12th 1935, in order to protect the coastal fisheries, were declared not to be contrary to international law.

Besides the demanding work on the international arena, Rollefsen had projects in Norway that required his participation. One important task was to provide new facilities for the Institute. In 1960, after many years of planning and negotiations the Institute moved into a new building near the waterfront in Bergen harbour. This greatly improved the working conditions. Earlier the staff of about 70 were scattered in several houses, most of them in converted flats.

In 1950, following a lecture by Rollefsen, a committee established by Bergen Commercial Association promoted a collection of funds from private contributors and the planning of a public aquarium began. The aquarium was to be constructed in connection with the new building for the Institute of Marine Research. Rollefsen had in this way initiated a project he later followed up in every detail. The planning challenged both his artistic mind and biological knowledge. Right from the outset, he emphasized the importance of making the aquarium attractive to the general public, but at the same time making it suited for experimental purposes so that it thereby could serve science and the fisheries.

When Rollefsen in 1947 became the director of the Institute of Marine Research he needed in a great measure all the varied abilities he possessed. He had to lay aside his own research projects and devote himself to leading the Institute with all the administrative tasks this involved. Norwegian marine research was faced with extensive work after the war. Research on a wider range of fish species was required, and a closer contact between the scientists and industry as well as the general public had to be established. Moreover it was necessary to bring new methods and technical equipment into use in marine research. With the ideas Rollefsen has always had about fisheries investigations and their relation to the fisheries, he had the best qualifications to achieve valuable results within his field.

Rollefsen is a scientist and administrator with considerable scientific imagination. He also has a strongly developed sense of scientific accuracy and always stresses the integrity of research. At the same time, however, he is a true artist and combines an eye for artisticly and esthetical values with a creative imagination more forceful than usually found among scientists. These qualities of Rollefsen's character are not only noticeable in company with friends and colleagues, but are perhaps most clearly manifested by the creation of the Aquarium in Bergen. The Aquarium bears evidence of a successful combination of extensive knowledge about life in the sea, a thorough understanding of the technical problems involved and an ability to give the plans an artistic implementation. Through the Aquarium Rollefsen has brought the life in the oceans as close to man as technically possible, and at the same time given the

visitors an illusion of descending into the sea to there discover a completely new world.

Gunnar Rollefsen, an artist within his field, is gifted with personal talents which have influenced his work as a fishery biologist. His scientific papers, therefore, bear a very personal stamp and this holds for his work as administrator and head of the Institute as well. His manner of proceeding at conferences and meetings has always reflected his rich personality, and one has the impression that Rollefsen during all his work has managed to transform his own high hopes and plans into realities. Other scientists may point to greater practical implementations of their work, but few have like him been able to illuminate important aspects of life in the oceans.

Also as a writer and a lecturer he has shared his knowledge with many interested people, and his readers and listeners are not only found among persons associated with the fisheries, but include the general public as well. This part of his work reflects still other aspects of his distinctive personality.

For his important and varied work Rollefsen has been honoured in various ways. Thus in 1960 the University of Bergen conferred on him an honorary Doctor's degree for his contribution to scientific research. He has received the Knight's Cross, First class, of the Order of St. Olav of Norway, the Commander's Cross of the Swedish North Star Order, and the Knight's Cross, First Class, of the Royal Danish Order of Dannebrog. Of his honorary scientific distinctions may be mentioned the Hans Strøm Medal of the Academy of Ålesund Museum, the Gold medal of the Association for the Development of the Norwegian Fisheries and the Oscar Sund Price medal. Rollefsen is a member of the Norwegian Academy of Science and corresponding member of the Zoological Society, London.

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AN APPRECIATION

It gives me great pleasure as President of the International Council for the Exploration of the Sea, to express, on behalf of the Council, our deep appreciation of the life and work of our old friend Gunnar Rollefsen. Gunnar Rollefsen first attended the annual conferences of ICES in 1934 as an expert for Norway. He was a delegate in 1945 and, with the exception of 1951, from 1948 to 1961 also. He was elected a Vice-President in 1957 and First Vice-President in 1958. We all very much regretted when he had to retire from the Council in 1962 owing to ill health. Had he been able to continue I have no doubt he would have eventually been elected President. He was Chairman of the North-Eastern Area Sub-Committee from 1945 to 1954 and of the Gadoid Fish Committee from 1954 to 1959. Gunnar Rollefsen was, therefore, very much a "man of the Council".

At the annual meeting in Bergen in 1957 Rollefsen suggested that an approach should be made to the Danish Government with a view to having the Council accorded proper international status in Denmark. With George Lienesch of the Netherlands he and I interviewed the then Danish Prime Minister, who received us sympathetically, as well as a number of high ranking officials of the Danish Government. Eventually, as is common knowledge now, the Danish Government called a meeting to discuss a Convention which was ultimately signed and ratified by all member nations. In the 1964 Convention there was provision for a host agreement with Denmark and when I came to sign this on behalf of the Council I felt that I was usurping the place of Rollefsen, who had done so much to bring this matter to fruition.

Rollefsen's advice was frequently sought in the Council and he always made valuable contributions to the discussions of the many problems which confronted us. As Chairman of the Consultative Committee I valued his help in the work we had to perform, especially as the Council's

Contribution given in honour of Gunnar Rollefsen at his 70th birthday.

new relationship with the former Permanent Commission, established under the International Fisheries Convention of London of 1946 necessitated new thinking on many problems.

Shortly after the War when Rollefsen was seeking funds for his new institution and the aquarium in Bergen we were all enthralled by his vivid accounts of his search for new materials and for new ideas, of which he himself was never short.

He never hesitated to assist the young fishery scientist. I well remember visiting Bergen as a young student in 1936 when Rollefsen, a busy man preparing to go off on a cruise, devoted almost a full day demonstrating to me his interpretation of the reading of otoliths of cod.

His obvious enthusiasm for the job, whatever it might be, was infectious. Kindly, generous, hospitable in the extreme, a good companion Gunnar Rollefsen made many friends at our Council meetings.

The International Council for the Exploration of the Sea takes just pride in having had as one of its foremost members Gunnar Rollefsen who will be long remembered by all those who regard him as a friend. On behalf of the Council I wish to offer Gunnar Rollefsen our congratulations on his seventieth birthday and to express our best wishes to him for his future health and happiness.

Arthur E. J. Went
President of the International Council
for the Exploration of the Sea.

FiskDir. Skr. Ser. HavUnders., *15*: 114—127.

TRIUMPHS AND FRUSTRATIONS OF THE FISHERY BIOLOGIST

It is the fishery biologist's main duty to acquire knowledge on the causes of the fluctuations observed in the catches of fish and shellfish. Both in space and in time the catches may vary widely. Scientific analysis has revealed that both natural factors, as a rule beyond control by man, and the fishing industry, acting as extra predator, can be held responsible. A good quantitative insight in this complex matter requires knowledge on reproduction, growth, migrations, natural mortality, and fishery mortality in the species concerned. To achieve this, the fishery biologist should have the disposal of laboratory and research-vessel facilities, equipped with sufficient staff and apparatus, operating on the basis of an adequate budget, all this adapted to the character and extent of the natural range of the fish populations under consideration. There is something else required, not to be bought for money: a good dosis of enthusiasm to tackle the intricate problems both in the field and in the laboratory.

The results obtained step by step are not intended for the protection of nature or to prevent rare and interesting species to become extinct, but rather to lead the way towards a rational exploitation of the fish stocks. The scientist produces the material for a sound governmental management programme.

One should realize that the exploitation of the aquatic resources is of quite an exceptional nature: here one harvests jointly what nature produces voluntarily. For the terrestrial resources, both animal and vegetable, this system has been abandoned long ago, leaving out of consideration some forgotten corners of the world where human society still works on a truly prehistoric level. Agriculture and animal husbandry replaced the free exploitation of the terrestrial natural resources since time immemorial. All the major products of nature are nowadays grown

Contribution given in honour of Gunnar Rollefsen at his 70th birthday.

on privately owned plots in which one counts on due repression of poaching and other infringements. Tillage and manuring, control of predators, parasites, and diseases requires investment of money and labour, but the net results of all this fall in the hands of the farmer, gardener, cattle breeder, poulter or apiarist who works his own plot of land. Scientific advice helps him to increase the yield both quantitatively and qualitatively as well as to mechanize and industrialize his working.

How far the fishery lags behind in this respect! Fishing usually means little more than jointly harvesting what nature yields, and this not only in the open sea but also in territorial waters, and in most of the fresh water. For a very limited number of species, predominantly of a non-mobile nature, the big jump forward to real farming has been made. This involves abolishment of the former free fishery, putting the suitable areas into the hands of fish and shellfish farmers, and adequate policing; further, adopting appropriate cultivation techniques as well as control of predators, parasites, and diseases based on scientific information. In several cases striking results have been obtained, demonstrating that nature, left to itself, does not necessarily lead to the maximum production. The biological potentialities are often remarkably greater than fully natural conditions suggest.

Terrestrial experience indicates that adequate reglementation of a joint exploitation of resources of mobile species can lead to better annual yields and can prevent eradication of more vulnerable species. This experience has been applied in the field of fisheries, which gradually led to the following development:

I

Checking evident cases of wasteful exploitation such as use of destructive fishing methods leading to the untimely death of great numbers of immature fishes. Examples are the prohibition of the use of explosives and poison, and the abolishment of fishing for young specimens of commercial species for the purpose of manuring the land. Though introduction of such measures seems a rather obvious matter, hardly requiring scientific advice, we have to admit that it was not so very long ago that one ruthlessly and purposely fished for immature fish in the nursery areas in inshore waters of the North Sea. The Government concerned (Netherlands) found it a difficult decision to put those trash fishers out of business even though it was clear that the benefits for the offshore fishery for consumption fish, in which more than one nation participates, would largely surpass the immediate losses.

II

A further step towards a more rational exploitation of the aquatic resources was the introduction of minimum legal sizes for species of commerical importance. Everywhere one noticed that large, presumably older, specimens invariably became scarcer according as one fished more intensely. Fishery biologists pointed out that in many a case fishes were harvested before they could participate in reproduction. Would this be done on too large a scale, there would be reason to fear that the level of reproduction could be drastically reduced, especially in fish populations with a limited range. It was not difficult to determine at which length the species under consideration becomes sexually mature, and hence to establish a minimum legal size permitting a fish to reproduce at least once before being caught.

Since taking such measures requires only a limited amount of scientific information, and since a minimum legal size is rather easy to control, one would expect that all modern countries had adopted this system long ago, in an effort to safeguard their aquatic resources both in fresh water and in the sea. Unfortunately this is not the case:

A) One can point out many a case in which governments are reluctant to adopt such a minimum legal size because the species under consideration are of considerable commercial interest before they attain sexual maturity. In such cases fishermen strongly oppose introduction of a minimum legal size based on this principle, and will abuse such a measure whenever possible if their government imposes it on them.

B) In case feeding habits are such that one strongly prefers the very young stages above exploitation of the larger fishes, few countries are willing to introduce a minimum legal size for such a species. Therefore one still fishes on a large scale for elvers in countries where the larger eels are less appreciated.

C) The same happens when the species under consideration is only within reach of the national fleet when immature, to migrate to other areas at a more advanced age.

D) Fish is often used as raw material for the production of fish meal, a crude product which finds its way predominantly to poultry farming and pig breeding. This is a sound principle when species are used which are in no developmental stage interesting as human food. Still, one can adduce quite a few examples in which the contrary is the case. When one started the production of fish meal from immature specimens of commercially important species, one often assumed that the stocks were so great that some thinning out of the schools of juveniles would not noticeably affect the catches of mature specimens (e.g. North Sea herring).

Another case is that of the brown shrimp for which one assumed that the small specimens were all males and would never grow up to commercial size, hence could safely be used as raw material for fish meal. We now know that this is not true, and that protection of small shrimps will lead to a noteworthy increase in the catches of larger shrimps. Still, it seems difficult to suppress the established shrimp meal plants, even when this would be financially very interesting for the shrimp industry as a whole.

III

Fishery biologists continued their scientific work and gradually managed to get a grip on the dynamics of aquatic resources, considering man as an extra predator. Quantitative information on reproduction, growth and mortality formed the basis of this better knowledge and mathematics helped to build up the fishery theory. It appeared to be necessary to collect information on reproduction, growth, and mortality for every species separately and often within one species for every separate population. It then became clear that a minimum legal size based on attainment of sexual maturity was a rather primitive tool in fisheries management. If sufficient knowledge was acquired for a given species and population, one could calculate how the fishing industry could make the highest catches in such a manner that it would not adversely affect the catches to be made in future years. This is the " optimum sustainable yield ". It appeared to be possible to indicate rather precisely at which size the fish could best be harvested if one is really after the highest catch, expressed in tons of fish. For both social and commercial reasons it is as a rule wise not to catch the whole year-class in too short a span of time, therefore to start fishing some time before the calculated size has been reached, and to continue fishing for some time after that supreme moment. The biologist is further acquainted with the often considerable fluctuations in the strength of the consecutive year-classes, and can give advice how to avoid too strong a reflexion of these fluctuations on the market through harvesting of several year-classes simultaneously.

It was the fishery biologist's pride and joy to be able to provide the material for a sound fishery management leading to a high and sustainable level of production. His advice could be translated to minimum legal sizes (often considerably higher than those formerly based on attainment of sexual maturity) and hence on the type of gear (e.g. mesh size of nets) to be used at a given level of fishing intensity. The biologist demonstrated how one can catch more fish by adoption of larger mesh

sizes, and when the fishery intensity is already too high, how one can catch more fish by reducing the fishery intensity, which means increase of the catch per "unit of effort". The best results will be obtained if the fishermen concentrate their efforts on one single species and avoid mixed catches as far as possible. To attain this, the biologist tries to gain more information on the behaviour of the fish to enable the technical experts to develop specialized apparatus and gear to find and to catch the species under consideration. Meanwhile he goes on collecting information on year-class strength, growth, and mortality in species of commerical importance, for these are data influenced by a variety of factors, man's activities included.

It must be possible to build up a sound fishing industry on the scientific basis produced by the fishery biologist. For obvious reasons, this goal will be reached easier in waters over which the government has complete jurisdiction, and somewhat more difficult in international waters. But there too it is in principle possible to come nearer to the optimum sustainable yield provided one manages to develop a good system of international control on the measures jointly taken. In Europe it was the setting up in the year 1946 of the Permanent Commission for the Overfishing of the North Sea, which promised international agreement on the measures to be taken for a sound management of the marine resources in the North Sea and adjacent waters. Later, its range was considerably broadened by the rebaptism into the North East Atlantic Fisheries Commission, on which occasion the measures to be discussed went far beyond establishment of minimum legal sizes for fish and for the mesh size of nets.

Were the high hopes nourished by the fishery biologists of many a nation justifiable? Three examples, one from outside, two from inside the NEAFC area, will elucidate this question:

A) The post-war revival of the Antarctic whaling industry was spectacular. An international commission had to watch against possible overfishing of the whales. Whales reproduce but slowly and the scientists had to admit that a fool-proof system of age determination in whales had still to be developed. Hence data on growth and on reproduction rate should be handled with caution. One could agree on a minimum legal size and on a system of annual quota, expressed in " blue-whale units ". When the catch per unit of effort began to decrease, the countries interested in whaling refused to believe in overfishing.

The scientists, realizing that the data on which they had to base their conclusions were not so dependable and complete as they would have wished, worded their reports with the under such conditions customary caution, which led the representatives of the industry to wave all their

apprehension aside. In a later phase all one was willing to agree on was a very slight reduction in the annual quota, so slight that it would have been virtually impossible to determine whether this reduction would have any effects at all. The reducing stock made remunerative exploitation soon impossible for the western countries. Perusal of the scientific information available leads to prediction of the number of decades required for the rehabilitation of the stocks if one stopped whaling completely and immediately. This forecast shows whaling cannot be a profitable industry for a long time to come. One also concluded from the available data that one had trusted in the overall observation of the minimum legal size one had agreed upon, but that evidently a great number of whales must have been stretched administratively.

This is a sad and disheartening story, especially for those who believe in a rational exploitation of marine resources based on scientific evidence.

B) Cod and haddock once abounded in the Barents Sea and adjacent waters. In the old days it were especially the Norwegian fishermen who caught the adults during their spawning migration to the Lofoten area. Later, a trawl-fishery evolved in the Barents Sea itself. The mesh size of the nets in use was rather small, and the fish got less chance to reach an appreciable size according as the fishery intensity increased. The fishes caught showed a gradual decline in average size and the catch per unit of effort decreased alarmingly. Scientific evidence collected by fishery biologists clearly showed what happened, and one finally agreed to use larger mesh sizes to protect the younger fishes. As usual, the industry tried to compensate for the declining catches by increasing the fishing effort. Thus the positive effect of the increase in mesh size is easily obscured. Another adverse effect of an increased fishing intensity is a reduction in the number of year-classes caught simultaneously. The fluctuations in the strength of the consecutive year-classes are as a rule considerable in gadoid fishes. Therefore, some degree of stablization in the annual catches can only be achieved when a greater number of year-classes is found in the cod ends of the trawl nets. One strong year-class may predominate in the catches for several years in succession. The smaller the number of year-classes caught simultaneously the greater the chance that there is sooner or later no rich year-class available at all, which makes the annual catches drop alarmingly. It is often assumed that the number of eggs produced in the spawning season is never a limiting factor in reproduction in fishes such as gadoids, which produce a great number of small-sized eggs. Still, unless the amount of food for the larval stages is the limiting factor in reproduction, it is hard to see how a considerably reduced number of eggs spawned (e.g. because only

a small number of adults participates in reproduction) will on an average lead to the same year-class strength as in periods with a more ample egg production. Fishery biologists from several countries have now stated that the stocks of cod and haddock in the North East Atlantic's Arctic section have come down to an alarmingly low level. The year-classes which will enter the fishery in the years to come are so poor that the annual catches in this area will drop to an unprecedented level. One hopes that a rich year-class will be produced in 1969 or 1970 so that the catch will improve in due course, but the small number of adults which will participate in reproduction in those years make many a biologist wonder whether the chance for a really good year-class to spring up is not very small, indeed.

Trawl-fishery will not be remunerative in this area for at least several years to come, and the number of fish migrating to inshore waters will no doubt be small for a longer period. What will the industry do? The fertility of the sea is not adversely affected by the fishery, and even very seriously reduced fish stocks will get a chance to recover when left in peace for several years. There is little hope that the countries concerned will agree to stop the fishery in this area to give the stocks a chance to recover, or even to reduce the fishing intensity drastically, to achieve the same goal somewhat slower. At most one is willing to restrain from a further increase in fishing intensity. The disappointing catches will sooner or later force the larger units to try their luck elsewhere (increasing the fishery intensity there), whereas the smaller vessels, operating inshore, will not be in a position to escape, and have to face disaster.

This, too, is a sad and disheartneing story, especially for those who produced the scientific material on which a sound management could have been based timely, and who welcomed the international agreement to increase the mesh size as a first step in the right direction, only to see later that one is unwilling to control the fishing intensity.

C) Herring has for ages been the most important fish in the North Sea, and for some countries the herring fishery was traditionally the most important section of the sea fishery. Herring used to be superabundant in the North Sea, and the total annual catches fluctuated but slightly. Fishery investigators used more of their time for the study of other species of fish, since the herring fishery gave no reason for concern. When the Permanent Commission for the Overfishing of the North Sea started its work, the herring was not listed among the protected species, and neither did one consider a minimum legal size for the herring or a minimum mesh size for the herring nets. Scientific evidence demonstrated that the catches were usually composed of a great number of year-classes, among which

one or more strong year-classes dominating in the catch pattern for years in succession.

In the post-war period the fishing effort gradually increased in the North Sea. More and/or greater ships and stronger engines came into use, electronic apparatus to find the fish schools were introduced, active fishing (trawl nets) replaced the passive gear (drift nets). The total herring catches from the North Sea remained after an initial increase at about the same level, despite the strong increment in fishing intensity. Analysis of the catches revealed that they were no longer composed of 10 to 12 year-classes, as in the past, but of fewer and fewer year-classes. In recent years it is virtually the year-class entering the fishery for the first time (the recruits, 3 years old) which dominates in the catches. Hence greater fluctuations in the annual catches in our time and the risk that some poor year-classes in succession bring down the total landings from the North Sea to an unprecedented level. The Downs stock, the herring population which always gave rise to an important fishery in the southern North Sea in autumn, and which spawns in the Channel towards the end of the year, suffered so much from the high fishing intensity that the fleets found it in recent years hardly worth while to continue fishing on it.

The growing concern in the herring sector led to international efforts to elucidate the causes of the decline of the herring stocks. One was in the beginning very reluctant to admit that the increased fishing intensity had anything to do with it. One rather blamed adverse weather conditions and unusual hydrographical patterns for the poor recruitment. An international tagging scheme should throw more light on the effect of fishery for young herring carried out in the German Bight (the Bløden fishery) has on recruitment of adult herring, and hence on the catches of herring for human consumption. The Bløden fishery produces raw material for fish meal plants in Denmark and Germany. Though herring has many natural enemies it cannot be denied that fishing away of great numbers of young immature herring must have some adverse effect on the stocks of adult herring. The tagging results seemed to warrant the conclusion (1957) that only some 15% of the immature North Sea herring fell victim to the Bløden fishery. Hence, the Bløden fishery can only be held responsible for a reduction in the catch of adult herring up to 15%. Just now, tagging of immature herring is undertaken on a larger scale, to find out whether the 1957 conclusions can be corroborated. However this may turn out, it seems always an unwise mangement to use young individuals of a fish species which is in adult stage fit for human consumption as raw material for the production of fish meal or other low-level products.

The situation aggravated when an improved fishing technique (the purse seine) made it possible to catch entire schools located with the aid of electronic equipment. Though a better fishing technique is in principle always welcome if it means less labour and lower expenses to catch a given quantity of fish, there was reason for serious concern in this case. The fish caught in large quantities could not get appropriate treatment on board of the ships and was, when landed, only fit as raw material for fish meal plants. Thus only a small percentage of the fish protein will indirectly—through mediation of chickens and pigs—come as human food on the market, though there would have been an excellent direct market for the herring itself. This sharp increase in the herring fishing soon led to a noteworthy reduction of the stocks and now the purse-seiners are in search of juvenile herring, which means destruction of still greater numbers of herring than at the time one found adult herring in sufficient quantities.

The situation is alarming for the strength of the year-classes which will recruit now and next year is very disappointing, indeed. The large-scale destruction of young herring continues. So much money has been invested in this industry that one is not inclined to consider to stop using herrings as raw material for the production of fish meal. On the contrary, one will fish with increased effort when the catch per day fishing is insufficient.

When the herring is left in peace, it can be expected that new stocks build up again, provided another species—like for instance the sprat—has not taken its place and its food, which phenomenon has been observed after heavy fishing on sardine stocks off the coasts of California and South Africa. In such cases the old situation may never return.

This again is a sad and disheartening story. Fishery biologists of all countries concerned agree now that herring can suffer from overfishing, and that it is unwise to reduce the stocks so much that the annual catches virtually depend on the strength of one or at most two year-classes. Use of food fishes as raw material for a fish meal industry seems very unwise, indeed. Everybody waits for a miracle and points out that dramatic changes in the herring population have been recorded from past ages. Nobody is really inclined to reduce the level of this herring fishery drastically to give the herring a chance to recover. Whenever there are signs of recovery, like was the case in the southern North Sea in 1968, one jumps immediately on it with a great number of ships, instead of exerting one's efforts to assist the stocks to come back to the old level.

No small wonder that the fishery biologist suffers from frustration. Did not he produce the scientific basis for a wise fisheries management,

and did not he put down in exact figures how one could reach the optimum sustainable yield for a given body of water or, if one preferred, the optimum sustainable profit? This optimum sustainable yield appeared to be a fata morgana. Many efforts were made to come closer and closer to this ideal situation. International agreement has been reached on the use of larger mesh sizes, and a system of international control was worked out step by step. But one did not reduce the number of fishery units according as the efficiency of these units went up.

One did not even seriously consider to prevent a further increase in the fishing intensity. The effect of mesh size increase is nullified by increment in fishing intensity and the desired stabilisation of the annual catches can only be reached when the fishing intensity is brought down to such a level that more year-classes are caught simultaneously.

Did the biologist fail to explain in clear terms what would happen if no concerted action was taken? Did he word his conclusions too cautiously so that all one wanted to do was asking for more detailed studies to clear up the points on which he expressed some doubt? The biologist certainly underestimated the resistance of economical and political nature. Reducing the fishing intensity means that capital already invested in ships and plants will be annihilated. One will prefer to continue working with a smaller profit or to ask for governmental subvention in some form or another. Politically it is difficult to prevent noteworthy numbers of employers and employed to continue their activities in such a specialized industry as the fishery is. Here, too, governments prefer to subvent the fishing industry and to cherish the hope that things will take a favourable turn.

What will happen now that the fata morgana called "optimum sustainable yield" seems more unattainable than ever? The sea fishery will in all probability split up in four directions:

A) The *tramp fishery*, a form of free enterprise not hampered by restrictions, which hunts for fish wherever fish can be found and wants to use all conceivable technical means to catch that fish. This form of fishery does not worry about the future. If a fish population shows signs of serious overfishing, one goes elsewhere. Distance should not hamper, therefore larger units equipped with facilities for deep-freezing, which can stay away from their home ports for weeks and months, are required. Whenever a stock of predatory fish is depleted, and nature, abhorring a vacuum, puts large schools of cephalopods in their place, one will fish for those squids and cuttlefishes instead.

Such a tramp fishery is already in existence and countries where wages are relatively low and/or where the sources of food rich in animal protein are scarce, will be in the best position to continue the tramp

fishery on a remunerative basis. The countries of western Europe will certainly not be among those who can easily compete in this field. The assistance of fishery biologists will only be invoked for this type of fishery to scout for fish schools, to follow their migrations and to develop efficient methods to catch the fish, based on detailed knowledge of their behaviour.

B) A type of fishery which could be described as *managed fishery*. The highest yields over a longer period of time can no doubt be expected from a given fish population if it receives proper management from the larval phase of the fish till the day of capture. This includes safeguarding spawning grounds and nursery areas from the adverse effects of pollution; keeping losses by predation within bounds as far as possible; protecting the young fishes against the danger of being caught in small meshed nets such as used by shrimpers; avoiding of wasteful fishing methods; catching the adult fish with nets of which the mesh sizes are scientifically prescribed so that one approaches the optimum sustainable yield as close as possible; and above all avoidance of a fishery intensity greater than strictly necessary. Proper management of a fish population is theoretically so attractive, since it promises the optimal use of the fertility of the sea and a minimum of fluctuations in the annual landings, that many a country will continue its efforts in that direction, despite the many disappointing experiences encountered thus far. The more countries participate in the fishing on a given population, the more difficult it is to agree on the necessary management measures. Palliatives will never lead to proper management. Since control of the fishing intensity on an international basis is not only the most important measure to be taken, but also the most unpopular and legally the most difficult, it is to be expected that countries, which want to make a serious effort in the direction of a managed fishery, will sooner or later follow other paths. Most probably the only way out to higher yields and more stabilized landings at a moderate fishing intensity will be proclamation of territorial rights so far offshore that the fish populations under consideration do not surpass those boundaries during their migrations. This may in due course lead to a sharing out of fishing grounds, as has already been done for the mineral resources on the continental shelf. Such a system requires the same rigid control as now applied in the present narrow strips of territorial waters. Species such as sole, plaice, and shrimp are among the first to benefit from such a managed fishing pattern. Still, experience gained within national waters demonstrates that the control of fishing intensity based on the number of units, the size or horse-power of the boats, or the size of the nets to be used, is a very difficult and intricate matter and that there are many ways to get around

such regulations, sometimes even leading to loss of seaworthiness of the ships used. Concerted action of experts or various description will be required to develop a workable formula to control the fishing intensity.

The alternative is to work out a basis of quota. This is only feasible where the landings are to a high degree centralized and conscientiously recorded. A quota system has moreover the economic disadvantage that there will always be a rush to get within the shortest time possible the quantity of fish allowed, which leads to inefficient use of fleet and personal and to an irregular supply of the market, hence to lower prices.

For the fishery biologist such a trend towards a truly managed fishery is certainly most interesting. This will give him a fair chance to demonstrate that he is worth his money, for he knows that the yield will increase substantially if his proposals for regulation of the fishery are put in practice. Now his own government is free to impose the measures he deems necessary for a rational exploitation of the fish stock under consideration. He feels no longer frustrated because his scientific proposals are amended to such an extent in efforts to reach unanimous international agreement that the net results will hardly be measurable. He knows now, that the results of his painstaking efforts to evaluate the strength of the year-classes, to measure the growth of the fishes, to follow their migrations, to study their hazards, will be used efficiently and that the measures he proposes to increase the yield quantitatively and qualitatively, measures such as prescribing the number of fishing units required, defining the characteristics of the gear to be used, and protecting the young fishes on the nursery grounds, will no longer be nullified by an uninhibited increase in fishing intensity, and by destruction of countless immature specimens by an industrial fishery.

C) A third line, already in operation on some scale is *fish cultivation*. Instead of harvesting the mature fish as nature produces it, one keeps it for a longer or shorter period in confinement as private property. This can only be done in well-protected waters where only the proprietor has the right to fish and from which the fish cannot escape. Usually this means keeping the fish in denser concentrations than occur in nature, which involves a careful control of the oxygen level, of the food supply, and of predators, parasites, and diseases. In fresh water, fishes like carp and trout are produced on commercial scale this way, in sea water it is in the first place immobile species such as oysters and mussels which are cultivated. In this latter case one should rather speak of a semi-culture. One offers the shellfish a suitable substratum, protects them against predators, parasistes, competitors, and diseases as far as feasible, but one does not control their food supply. Dense concentrations of molluscan shellfish can only be grown successfully where tidal currents see to a steady

supply of the natural plankton. As a rule a semi-culture yields a far greater crop than nature would ever have produced without man's intervention, but one cannot step up the production beyond the ceiling set by the natural food supply.

A true cultivation of fishes in the marine environment, in which extra supplies of food have to be offered, has just been started. In the second half of the 19th century hatcheries have been set up in many a country in an effort to check the decline of the fish stocks by producing small fry of fish and lobsters, which was then brought back to the natural environment. This because one assumed that the earliest developmental phases might be the bottleneck determining eventually the strength of the fish stocks. That one hardly ever picked the fruits of these efforts should in the first place be ascribed to a lack of quantitative insight. We appreciate that one persevered until well in the 20th century, for psychologically spoken it must have given a great feeling of satisfaction to put out into the sea great numbers of young fishes in return for all the fish harvested commercially.

In recent years cultivation of marine fish has been resumed, first on experimental scale, later in pilot plants. One had in mind to rear young flatfish from the egg till "postage stamp" size, and then to transfer those young fishes to areas where flatfish food abounds, but where stocks of flatfish are virtually absent. Should the flatfish grow up successfully in these areas, then it had to be expected that fishermen from more than one country would try to harvest this bounty. In a later phase one diverted to rearing valuable flatfish species to consumption size. Warm water discharged by electric plants could be used to speed up the growth of the fishes. It remains to be demonstrated whether production of valuable species of consumption fish can be remunerative in such plants. If so, application can be expected in several countries possessing well-sheltered sites with unpolluted and undiluted sea water.

The fisheriy biologist interested in cultivation projects will find a rich field for his activities here. He should evaluate all environmental factors involved in cultivating dense stocks of fish in captivity, should work out a suitable diet which promotes growth of the fish, which food should be relatively cheap and to be kept in stock, and should study parasites and diseases which could cause harm, and develop methods to control those.

D) The fourth line in the sea fishery could be described as the *sport-fishery*. Already now sportfishermen turn more and more to the sea, not only because many fresh waters become so badly polluted that sport-fishing is hardly longer possible there, but also because boats and equipment required for sport-fishing in sea gradually come within reach of a

greater number of people. Sport-fishing can be of considerable recreational and economical value for a country, but that not in the first place because of the consumption fish caught. The fish often comes in the last place and is not seldom left behind or displayed on the ship in such a way that it spoils. It is not important either what it costs to catch one fish. Especially in tropical and subtropical countries sport-fishing in sea will show a rapid increase and exert a greater economical impact than the commercial fishery ever did there.

The fishery biologist can assist the development of the sport-fishery by providing information on the migration of the species concerned and by disseminating knowledge on the habits and whereabout of the species the sportfisherman is interested in. Sport-fishing contributes to the fisherman's happiness and well-being, partly because of the nostalgia a man in a modern civilization feels when he thinks of his ancestors in ages long gone by, trying to squeeze a living out of the hostile waters by outwitting the denizens of the sea. And thus prehistoric times merge into our modern world.

Will all this really happen, which means radical changes in the present fishery pattern, and disaster in many of its sectors? In principle a joint fishery on a truly rational basis does still belong to the possibilities, but if one seriously wants to reach that goal a rapid and drastic change of gear is a prerequisite. The fishery biologists are certainly ready to take up the challenge.

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STUDIES ON BLOOD PROTEINS IN HERRING

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INTRODUCTION

An investigation on blood proteins of herring, *Clupea harengus* L., was started in 1965 in order to find characteristics to be applied on the problem of identification of stock units. As part of this programme a report on serum esterase polymorphism has been published (Nævdal 1969). The present report deals with the electrophoretic analyses of hemoglobins and serum proteins. A complete description of ontogenetic variations in herring hemoglobin has been published (Wilkins and Iles 1966), and in the present report most attention has therefore been paid to the serum proteins.

MATERIAL AND METHODS

Blood sampling, treatment of blood and sera, analyses by electrophoresis, staining of proteins, autoradiography etc. were carried out in the same way as described for investigation on sprat (Nævdal 1968). Parker and Bearn (1963) and Cann (1966) found multiple electrophoretic zones rising from protein-buffer interaction in the presence of boric ions. The buffer used in the present routine analyses contained boric acid, and to find out whether boric ions had any influence upon the protein zones, part of the material was analyzed by a buffer without boric acid but otherwise under identical conditions.

The type of herring investigated, date and locality of sampling and numbers in the samples are listed in Table 1. Age, sex, vertebrae numbers and otolith and scale type have been determined for part of the material. The specimens of samples 9 and 10 were caught as 0-group in August 1965 and separated into two batches which were kept isolated in tanks under simulated North Sea and Barents Sea temperature conditions (Haraldsvik, personal communication).

Contribution given in honour of Gunnar Rollefsen at his 70th birthday.

RESULTS AND DISCUSSION

BIOLOGICAL VARIATION

Hemoglobin

The results of the hemoglobin analyses were, except for insignificant differences, in accordance with the ontogenetic variations described by Wilkins and Iles (1966). The relationship between hemoglobin types and growth may be different in the various populations, but as long as this is not completely understood, hemoglobin types cannot be used for identification of stock units. Therefore a further discussion of the hemoglobin types have been omitted.

Serum proteins

All serum proteins moved towards the anode at pH 9.0. Considerable variations were noted in several groups of proteins. A representative selection of protein patterns (electrophoretograms) are shown in Fig. 1.

The serum transferrins, identified by autoradiography, had less anodic mobility than any other serum proteins. Two transferrin bands were common. They were named Tf A and Tf B, the first had the greatest anodic mobility. Each specimen might possess one or two of the transferrin bands, and the phenotypes were named Tf AA, Tf AB and Tf BB according to the components they possessed.

Specimens which contained a single strong transferrin band only, often showed a faint band at the position of the lacking transferrin band

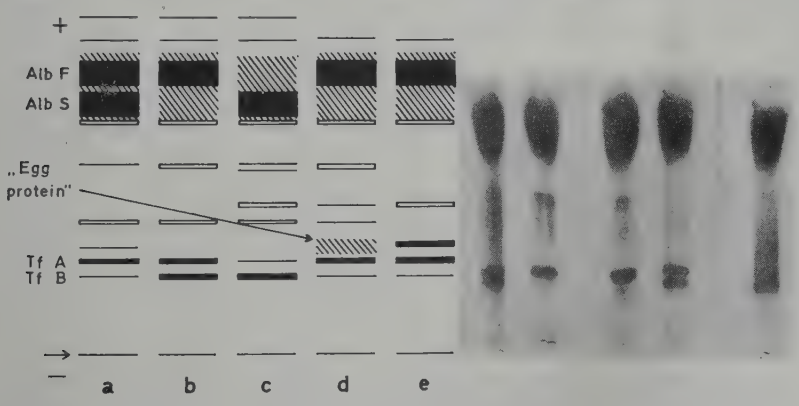

Fig. 1. Outline of serum protein patterns in herring obtained by combined starch and agar gel electrophoresis at pH 9.0, and photograph of electrophoretograms obtained by routine analyses. Filled in bars: Strong bands. Hatched bars: Moderately strong bands. Single lines: Faint bands. The point of application is indicated by the smaller arrow. From left to right the photographed types are: Tf AB, Tf AA, Tf AA, Tf AB, and Tf BB.

(Fig. 1). These specimens were classified as if the weak band was absent (Tf AA or Tf BB phenotype). The faint bands varied in strength among specimens and sometimes even between repeated analyses of the same specimen. The determination of the transferrin phenotypes were consequently to some degree unreliable.

A few specimens had one band close to Tf A at the cathodic side. A fourth band, seen on the anodic side of Tf A in a few specimens, probably represented a second rare transferrin component (Fig. 1e). The two rare bands were not tested autoradiographically since sera were not available when the tracing experiments were made, and they were both classified together with Tf A when calculating frequency distributions.

Presence of great amounts of hemoglobins in the serum slowed down the mobility of the transferrin molecules, especially Tf A, and consequently several specimens might be incorrectly determined as Tf BB. The relation between hemoglobins and transferrins was not clear, but the transferrins did not stain with *o*-dianisidine and consequently had no hemoglobin-binding capacity. Evidently sera containing considerable amounts of hemoglobins could not be used for determination of transferrin types.

Freezing and thawing of sera had no influence on the mobility of the transferrins or other serum proteins. However, a prolonged storage of sera in deep freezer had a similar effect on the transferrins as the presence of hemoglobins, namely reduced anodic mobility, making the type determination unreliable.

A broad and diffuse band was found on the anodic side of Tf A in females near spawning. Position and strength differed, but it was always located near Tf A, and therefore the classification of transferrin types in these cases was difficult. This band probably represented the "ripe female protein" observed in species of the genus *Oncorhynchus* (Tsuyuki and Roberts 1966) and the rainbow trout, *Salmo gairdneri*, (Thurstone 1967).

Several protein bands were seen between the transferrins and the albumins. Although great variations were observed, these bands were too weak or too diffuse to form the basis of classifying the specimens into well-defined groups. Some of these patterns are outlined in Fig. 1. Since one of the mentioned bands stained with *o*-dianisidine, it probably represented haptoglobin/hemoglobin complexes.

Two main albumin components could be distinguished. One or both were present in each specimen (Fig. 1). The faster moving component was named Alb F and the slower Alb S. The three phenotypes were named Alb FF, Alb FS and Alb SS. The differences between the albumin types were often insignificant, and accordingly the albumin type determinations could only be accomplished in a few samples. In front of the albumins one or two faint pre-albumin bands were observed.

Table 1. Observed distributions (obs) of transferrin types in herring compared to expected Hardy–Weinberg distributions (exp).

Sample no.	Locality and date of sampling		Indications of sample		Transferrin groups Tf AA	Tf AB	Tf BB	No.	q_A
1	Håvik i Fusa, Hordaland	5 Oct. 65	O-group	obs	60	17	1	78	0.88
				exp	60.4	16.5	1.1		
2	Fensfjorden, Hordaland	15 Oct. 65	O-group	obs	57	24	17	98	0.70
				exp	48	41.2	8.8		
3	Fensfjorden, Hordaland	23 Oct. 65	O-group	obs	86	20	4	110	0.87
				exp	83.3	24.9	1.9		
4	Buagrunnen, off Møre	10–11 Febr. 66	Adult Norwegian spring spawners	obs	196	124	17	337	0.77
				exp	199.8	119.4	17.8		
5	Røstbanken, Lofoten	10 March 66	Norwegian spring spawners	obs	68	33	8	109	0.78
				exp	66.3	37.4	5.3		
6	Fanafjorden, Hordaland	14 April 68	Adult spring spawners	obs	43	50	20	113	0.60
				exp	40.7	54.2	18.1		
7	57° 40′ N, 04° 30′ E North Sea	24–25 May 66	Autumn spawners	obs	14	55	83	152	0.27
				exp	11.1	59.9	81.0		
8	58° 00′ N, 05° 00′ E North Sea	27 June 66	Autumn spawners	obs	17	38	23	78	0.46
				exp	16.5	38.8	22.7		
9	Lysefjorden, Hordaland	18 Aug. 66	See text	obs	12	51	35	98	0.38
				exp	14.2	46.2	37.7		
10	Lysefjorden Hordaland	23 Aug. 66	See text	obs	12	46	38	96	0.36
				exp	12.4	44.2	39.3		
11	Myking, Hordaland	April 67	Adult spring spawners	obs	37	33	13	83	0.64
				exp	34	38.3	10.8		
12	Duesund, Masfj. Hordaland	12 June 67	1-group	obs	69	25	2	96	0.85
				exp	69.4	24.5	2.2		
13	Halifax, N.S. Canada	June 68	Adult	obs	74	20	4	98	0.86
				exp	72.5	23.6	1.9		

None of the observed variations could be correlated with age or sex, except for the "ripe female protein".

The variations also occurred when boric acid was omitted in the buffer. Therefore the observed variations cannot be due to a protein-buffer interaction caused by boric ions. However, it is possible that other substances in the buffer or medium may interact with the proteins and thus cause artificial multiple zones.

Two allelomorphic genes (named Tf^A and Tf^B), each controlling one transferrin component, would explain the intraspecific variation in the herring serum transferrins. This corresponds to the transferrin variation in cod (Møller 1966) and in some other gadoid fishes (Møller and Nævdal 1966). The observed distributions of transferrin types in herring are shown in Table 1, and assuming the above gene combinations, gene frequencies were calculated from the observed distribution in each sample. Good agreements between observed and expected distributions were found in most cases. The deviations were not statistically significant, except for sample 2. This sample, which showed an excess of hypothetical homozygotes compared to expected numbers, might represent a mixture of two or more populations. Consequently, control by two allelomorphic genes may be accepted as an explanation of the herring transferrin variations.

The rare transferrin components are believed to be controlled by other alleles belonging to the same genetic system. However, because these components occurred only in a few specimens, this hypothesis could not be tested statistically. The presence of weak components in addition to the stronger transferrin components do not necessarily cause any difficulties in explaining the transferrin variations in herring. Simultaneous variation of a major and a minor component has been reported for the serum transferrins in mouse (Schreffler 1960), and the herring transferrins may be controlled in a similar way. However, the minor components of the mouse transferrins were invariably present, whereas in herring they might differ in strength and even be lacking. This indicates a more complicated genetic control by modifying genes or dependence upon non-inherited factors.

The albumin variations may also be controlled by two alleles, each controlling one main albumin component. In the few samples where the albumin types could be determined with a reasonable degree of reliability, fairly good agreement was found between observed and expected distributions. Consequently, the albumin variation in herring and its control may be similar to the albumin variation in man (Knedel 1958, Efremow and Brænd 1964), chicken (McIndoe 1962), and horse (Brænd 1964).

No hypothesis of genetic control of the other serum protein variations can be put forth due to the protein bands in all cases being too weak for proper classification.

GEOGRAPHICAL VARIATION

Assuming that the hypothesis of genetic control of the transferrin types in herring is correct, their frequency distributions may be used for identification of population units. The variations in the other blood proteins are at present not revealed clearly enough to be of any value for this purpose. Table 1 gives observed distributions of transferrin types and the frequencies (q_A) of the hypothetical gene Tf^A, taken as a characteristic sample parameter. All these samples have been analyzed fresh or fresh frozen, and sera with considerable amounts of hemoglobins have been omitted. Due to difficulties caused by the weak transferrin zones, statistical methods for comparing samples have not been applied. However, the considerable variations of q_A among samples may allow some tentative conclusions.

The highest value of q_A was found in some samples of young herring from inshore waters of western Norway (samples 1, 3 and 12). Sample 2 collected in the same area and approximately at the same time as sample 3, showed somewhat lower q_A-value, and the distribution of phenotypes in this sample was not in accordance with expected Hardy–Weinberg distribution, indicating a mixture of populations differing in q_A. The q_A-values of the samples 9 and 10 also indicate that herring of different origin is populating the inshore waters of western Norway. The herring in these samples had been caught in inshore waters south of Bergen and kept for one year at the Institute of Marine Research. These two samples of herring, exposed to different temperature conditions, showed nearly the same q_A-values. The values were much below the values of samples 1, 3 and 12, but similar to those observed in samples of North Sea autumn spawners (samples 7 and 8). The mean vertebrae number and otolith characters indicated that these young herring originated from North Sea autumn spawners (Haraldsvik, personal communication).

No significant differences were observed between the samples from the southern (off Møre) and northern (off Lofoten) spawning grounds of the Norwegian spring spawning herring, but differences should not be expected since the northern group was recruited from the southern area in 1959–61 (Devold 1968). The q_A-values of these samples were higher than for samples of mature spring spawning herring from inshore waters of western Norway south of Møre (samples 6 and 11). Differences have been found in age composition, scale pattern and growth rate between Norwegian spring spawning herring and spring spawners from inshore

waters of western Norway (Haraldsvik 1968). Samples 6 and 11 also differed from samples of young herring in the same fjords indicating that the adult and young herring in the same area may originate from different populations (local populations, spawning migrations of other populations and eggs and larvae from offshore waters).

In the two samples (7 and 8) of autumn spawners from the North Sea the q_A-values were significantly lower than for the other samples, but the q_A-values in these two samples did not agree. It is suggested that the samples consisted of a mixture of different groups of autumn spawners and this may explain the observed differences.

The sample from Canadian waters showed that variations in serum transferrins are present also in herring in the west Atlantic. The same phenotypes occurred as far as could be stated by the present electrophoretic methods, indicating control by homologous genes. The sample showed a gene frequency near the highest observed in samples from Norwegian waters.

SUMMARY

1. Hemoglobins and serum proteins of herring have been analyzed by agar gel electrophoresis (hemoglobins) and combined starch and agar gel electrophoresis (serum proteins). The material comprises twelve samples from the Norwegian coast and the North Sea and one sample from the east coast of Canada, a total of 1,546 specimens.
2. The results of the hemoglobin analyses were in general agreement with the ontogenetic variation described by Wilkins and Iles (1966).
3. Intraspecific variation was noted in the transferrin components. Three common transferrin types were found and assumed to be controlled by two allelomorphic genes. No relation to age or length was found. Presence of additional weak components complicated the type determination. Hemoglobins in the sera as well as prolonged storage made the type determination unreliable.
4. Observed albumin variations could be explained assuming control by two alleles, while observed variations in other serum protein groups were too weak or too diffuse for classification. A broad and diffuse band was found on the electrophoretograms from ripe females.
5. Considerable variations in the frequencies of the genes supposed to control the transferrin types were observed among samples. The type determinations were in some specimens complicated, but the observed variation were greater than what could be explained by incorrect type determination or sampling error. The variation therefore probably represent real differences among population units.

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BALANUS BALANOIDES (L.) ON THE ATLANTIC COAST OF FRANCE: FURTHER OBSERVATIONS ON THE SMALL ISOLATED POPULATION AT THE SOUTHERN LIMIT OF ITS DISTRIBUTION AT ARCACHON

By

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The behaviour of an animal near the limits of its distribution is always of considerable ecological interest. On western European coasts *Balanus balanoides* (L.) is one of the most common components of the littoral fauna of rocky and relatively open coasts (for a summary of the literature see Barnes 1957a, 1958, Barnes and Barnes 1962). In its distribution and behaviour it may be regarded as a typical boreo-arctic species, characteristics typical of a northern species accompanying it to the southern limits of its distribution (Barnes 1957b). It is present in quantity on the eastern Channel coast of France although much less abundant in the western channel; there seems, however, to have been an increase in population density in the western region during the past ten years (Barnes and Barnes 1966). On the French Atlantic coast it is fairly common, although somewhat unevenly distributed, with the southern limit in quantity at La Rochelle. There is then a complete break in the distribution with a reappearance in moderate quantity in north-western Spain, in the Asturias and Galicia. Some details of competition at Pornic, near to the southern limit, with the warm-temperate littoral *Chthamalus stellatus* have recently been given and an account of the effect of abnormal temperatures (Barnes and Barnes 1968).

Barnes and Powell (1966, *q.v.* for a discussion of the validity of some older records) have drawn attention to a small "isolated" population south of La Rochelle at Arcachon. Very small numbers were originally (in 1963) recorded on a concrete wall—one of the very few suitable areas

Contribution given in honour of Gunnar Rollefsen at his 70th birthday.

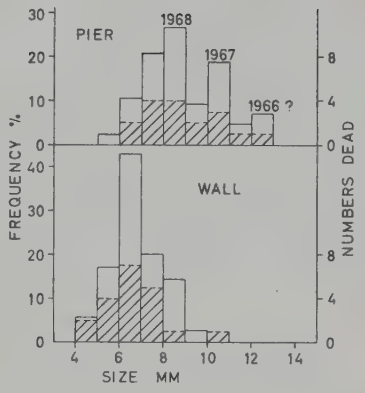

Fig. 1. *Balanus balanoides* at Arcachon; size (basal diameter)- frequency (%) distribution of animals in two localities, with estimated year classes on the pier; hatched area, size frequency (actual numbers) of empty shells.

in this locality—between the Jetée Anglais and the Jetée de la Chapelle; subsequently (in 1964) a few individuals were found on stakes from the Bassin itself. The animals on the wall were recorded as too far apart to breed and were estimated to be one year old; all were present under well-developed *Fucus vesiculosus* at about M.T.L.; by 1967 this population had markedly increased (Barnes and Barnes 1968). Those on the stakes appeared to represent two year classes and consisted of a small group of animals, all of which had well-developed egg masses.

Further observations on the "wall" population—the total lateral extent of which is about 1.0 km—are now recorded. The basal diameters of all the animals, living and dead (empty shells), found during a thirty-minute survey of both the wall and the piles of the Jetée Legallais were recorded. On the wall 35% of the population was dead, on the piles only 17%. The size distribution of each population is shown in Fig. 1. The wall population has a well-marked peak at a diameter of 6.0–7.0 mm which may be confidently assigned to the settlement of the spring of 1968; no further year classes can be recognized but a skewness to the right suggests the admixture of small numbers of an older year class; individuals larger than 10.0 mm were not found and all the evidence suggests that on the wall animals do not live beyond two years. On the piles the first year class is represented by the 8.0–9.0 mm size group; a peak at 10.0–11.0 (1967 spat) and possibly an earlier settlement can be recognized. Almost 30% of the pile population had a size greater than 10.0 mm and empty shells up to 14.0 mm were found. It seems clear that both survival and growth are better on the piles; this may be due to greater protection from high summer temperatures which would be inimical to an essentially boreo-arctic species.

The original records were for the wall; on that occasion the piles were

not examined carefully since at that time Mr. H. T. Powell's interest centred largely on the occurrence of *Fucus serratus* which is restricted to the wall. It seems possible that the piles were first colonized. The density is now sufficient to give an expanding but still very local population some of which settles on the nearby wall annually, and there lives only for about one year. In view of the distance from La Rochelle it is very unlikely that planktonic larvae are brought into the Bassin each year—even though this (or a vector from the same place) was responsible for the original colonization.

SUMMARY

Balanus balanoides is present as a small, isolated and even locally restricted population on the west coast of France at Arcachon. Observations of the past few years indicate an increase in numbers. Growth and survival are best in shaded places - possibly due to these affording some protection from high summer temperatures.

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NOTES ON GREENLAND HALIBUT, *REINHARDTIUS HIPPOGLOSSOIDES* (WALBAUM), IN THE EASTERN NORWEGIAN SEA

By

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DISTRIBUTION

Very little is known about the distribution and development of Greenland halibut, *Reinhardtius hippoglossoides* Walbaum 1792, in the Norwegian Sea and the Barents Sea. In the eastern Norwegian Sea the mature stock is distributed from the Norwegian coast along the slope of the continental shelf northwards W of Bear Island to Spitsbergen. Lower abundance is found off the coast of South Norway, and in the southern part of the Barents Sea eastwards to the Kanin Peninsula and the SW coast of Novaja Zemlya and at the coasts of Spitsbergen (Fig. 1). The species is rarely found in the Norwegian fjords. Greenland halibut is also distributed in the southern part of the Norwegian Sea between the Faroes past E and N of Iceland and the SE coast of Greenland.

In the fjords and along the coast of West Spitsbergen Greenland halibut was not very common in the first half of this century (Hognestad

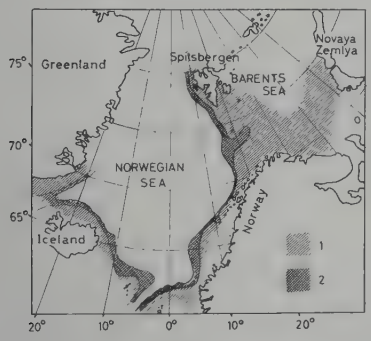

Fig. 1. 1 and 2. The distribution of Greenland halibut in the Norwegian Sea and the Barents Sea. 2. The area between 400 and 1000 m depth along the slope of the continental shelf.

Contribution given in honour of Gunnar Rollefsen at his 70th birthday.

1961), but later the abundance of young age groups seems to have increased considerably. The species was found in this area in 1946 and 1947 (Devold pers. comm.), and in 1958 young age groups seemed to be quite common in the fjords (Hognestad 1961). In recent years it has been frequently found in Spitsbergen waters. Young age groups (0–4) have not been found in other parts of the Barents Sea (Andriyashev 1954) nor along the Norwegian coast. Very little is known about spawning and development in this area, but some observations were made in 1964 and 1965 (Sorokin 1967).

An increasing Norwegian fishery is taking place in the eastern part of the Norwegian Sea from February to September at depths between 400 and 800 m. The fishing grounds are located along the slope of the continental shelf from off the coast of North Norway to off the coast of Spitsbergen. In the W–E direction they are located in a relatively narrow band due to the depth conditions along the slope (Fig. 1). Similar conditions are found along the slope of the continental shelf N of Iceland (Konstantinov 1968). Judging from the locations of the fishery from time to time, it seems that mature Greenland halibut migrate slowly from the area outside North Norway to the waters W of Bear Island and Spitsbergen from February to July. From the same area some migration takes place eastwards to the southern Barents Sea in the same period (Sorokin 1967) but this is probably mainly the immature part of the stock.

OBSERVATIONS ON O- AND I-GROUP GREENLAND HALIBUT

Bottom-trawling was carried out with R/V *Asterias* during the summers of 1958 and 1960 on the banks and in the fjords of West Spitsbergen both along the W and N coasts. Juvenile Greenland halibut were found in the fjords at depths varying from 190–300 m, and in temperatures between

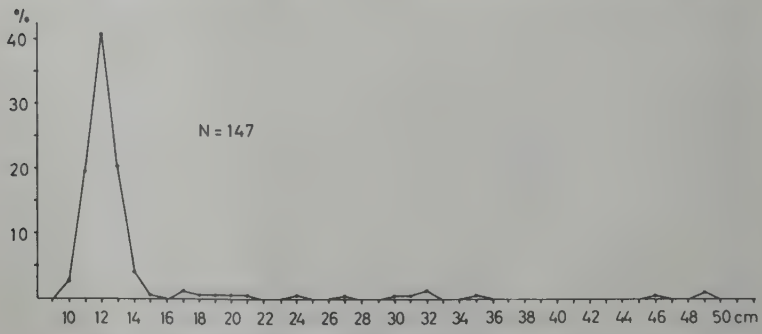

Fig. 2. The length distribution of Greenland halibut from the fjords of West Spitsbergen 1958.

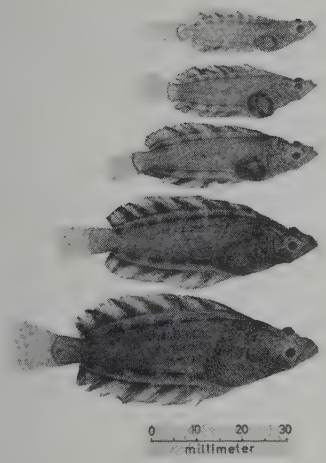

Fig. 3. O-group Greenland halibut of 36, 40, 47, 58 and 67 mm length from the Woodfjord, Spitsbergen, 10 August 1960.

—0.7° and 1.3°C, mainly around 0°C. The size distribution varied between 10 and 50 cm, but generally more than 90% of the catches consisted of fish of 10–15 cm length (Hognestad 1961, Fig. 2).

In August 1960 some O-group Greenland halibut of 36–67 mm length (mean 49.6 mm) (Fig. 3) were caught with mid-water trawl in Woodfjord on the N coast of Spitsbergen at 60–80 m depth (Fig. 4). Larvae of 36–40 mm length had not completed their metamorphosis, but showed signs of the imminent turning of the head. The larvae were half transparent, and their intestines were filled with red-coloured food, mainly small unidentified crustaceans. The temperature of the water layer where the larvae occurred varied from 1–2°C. Weak echo-recordings were made of a layer which consisted of planktonic organisms together with larvae of Greenland halibut, Long Rough Dab and Cottidae.

In 1966 a few O-group Greenland halibut were caught in early September with pelagic trawl at 25–35 m depth at almost 79°N, off the coast of West Spitsbergen (Fig. 4). In August–September 1968 some O-group Greenland halibut were taken with pelagic trawl both along the W coast of Spitsbergen and between Bear Island and Spitsbergen (Fig. 4). The catches were made at 10–50 m depth in temperatures from 0°–2°C. The highest abundance was recorded at approx. 78°N (Sentinellaflaket). The length distribution (Fig. 5) varied from 33–69 mm (mean 45.7 mm). The recordings in 1966 and 1968 were made during the combined

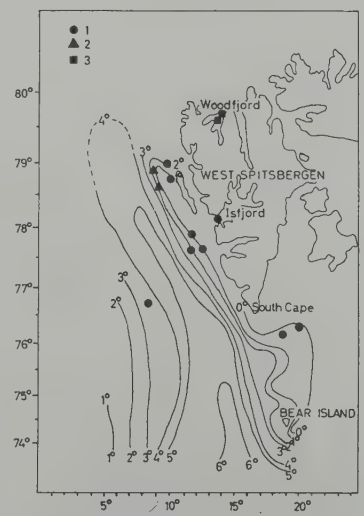

Fig. 4. Catch localities of O-group Greenland halibut in (1) 1968, (2) 1966 and (3) 1960. Isotherms at 50 m depth in early September 1968.

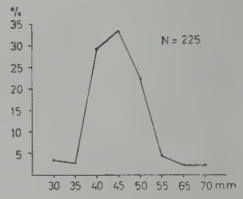

Fig. 5. The length distribution of O-group Greenland halibut from the Spitsbergen area August–September 1968.

English–Russian–Norwegian O-group fish survey in the Barents Sea. The above-mentioned observations of O-group Greenland halibut are the only ones known so far in the Barents Sea area.

DISCUSSION

The spawning and development of the Greenland halibut are described from West Greenland (Jensen 1935). In these waters spawning takes place at 600–1000 m depth in temperatures between 3.5° and 4°C and a salinity of 34.5‰. Assuming that the Greenland halibut require the same hydrographical conditions for spawning in the Barents Sea area, which means temperatures between 2° and 4°C, one can to some extent locate the spawning grounds in this area.

According to Andriyashev (1954) Greenland halibut migrate to 800–1200 m depth for spawning. At the eastern parts of the Norwegian Sea these depths are only found along the slope of the continental shelf from the Norwegian coast northwards to W of Spitsbergen. Along this slope the temperature as a rule decreases to 0°C at 800–1000 m depth (Helland-Hansen and Nansen 1909). This has also been shown by several observations during recent years. In the same area the 2°C isotherm is located at 600–800 m, but W of Bear Island it can be found at 300–400 m (Mork 1968). The temperature range 2°–4°C is thus generally found at 300–800 m depth along the slope from the coast of Norway to West Spitsbergen.

The finds of O-group Greenland halibut indicate that spawning must take place along the slope of the continental shelf between North Norway and Spitsbergen, and recent Russian investigations also seem to confirm this (Sorokin 1967). Judging from the locations of the temperature range 2°–4°C in this area, it is most likely that spawning takes place no deeper than 800 m.

The time of spawning in West Greenland waters is from April to June (Jensen 1935). In the eastern Norwegian Sea area it is supposed to take place from March or April to July (Milinsky 1944, Andriyashev 1954). The size of the O-group fish observed in August–September indicate that the main spawning takes place in April–June, but Soviet scientists have observed considerable spawning in November–December in the same area (Nizovtsev pers. comm.).

Off West Greenland larvae with yolk sac of 10–18 mm length are found at 600–1000 m depth. Larvae longer than 16 mm are found near

the surface and near land. The larvae are still bilateral symmetrical at a size of 54–57 mm. In August–September the larvae reach the length of 60–70 mm at which size the pelagical period ends and the larvae seek bottom life. At the same time pigmentation on the blind side disappears, and does not appear again until the fish reaches about 15 cm (Jensen 1935).

In the Barents Sea area young Greenland halibut (age groups 0 and 1) have been found in Spitsbergen waters only (Hognestad 1961, Fig. 4), and the development seems to be similar to that in Greenland waters. In Spitsbergen waters, however, the movement of the left eye probably starts before the larvae reach a length of 35 mm and is found to be completed on larvae of 60 mm length compared with 85 mm in Greenland waters. In both areas the larvae seem to reach the maximum pelagical size in August–September, but the metamorphosis is completed before the larvae seek bottom. The observations of the pigmentation are the same in Spitsbergen and West Greenland waters.

The smallest larvae hitherto found in the investigated area is 33 mm, and the reason for the lack of smaller sizes is certainly that investigations have not been carried out in the deep layers where Greenland halibut are supposed to spawn. The only area where I-group fish have been found is in inshore Spitsbergen waters. This indicates that the nursery grounds are located here, and a southwards migration takes place later on.

The main spawning grounds must be located along the slope of the continental shelf between 70°N and 75°N at 400–800 m depth, judging both from the distribution of the O-group fish and the hydrographical conditions. If spawning took place further to the S, O-group fish should have been observed in the Barents Sea as well according to the prevailing currents.

SUMMARY

The distribution of *Reinhardtius hippoglossoides* (Walbaum), Greenland halibut, in the Norwegian Sea is described with special reference to the distribution in the eastern part of the area.

The only records of O- and I-group Greenland halibut in this area are made in Spitsbergen waters.

The distribution of O- and I-group fish together with the hydrographical conditions along the slope of the continental shelf between Norway and Spitsbergen lead to the conclusion that the main spawning area of Greenland halibut must be along the slope between 70°N and 75°N in April–June at depths between 400 and 800 m.

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THE SCIENTIFIC NAME, DISTRIBUTION AND CHARACTERISTICS OF THE BLUE LING, *MOLVA DYPTERYGIA* (PENNANT), FROM WEST GREENLAND AND NEWFOUNDLAND AREAS

By

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INTRODUCTION

Morphometric characteristics have been described previously for only one blue ling from the western Atlantic (Templeman and Squires 1962) and meristic characteristics for only four, and two of these were described as *Molva molva* (L.) by Jensen (1948). Hence more morphological and meristic data are needed for comparison with specimens from the Northeast Atlantic. Data for three new specimens are presented (Tables 1, 2). Unless otherwise noted, morphometric and meristic data were obtained by the methods of Hubbs and Lagler (1958).

There is, moreover, considerable confusion regarding the scientific name of the blue ling and this subject is discussed and conclusions drawn.

Additional scientific records help to outline the present distribution of the blue ling in the western Atlantic (Figs. 1, 2, Table 3) and an attempt is made to bring order to the statistics of blue ling and ling as reported to ICNAF and to correct some of the major errors in these reports.

SCIENTIFIC NAME OF THE BLUE LING

Neglecting the previous period when even more variations of scientific names were used (see Svetovidov 1948 and Fraser-Brunner and Palmer 1951 for lists of these), in recent years two main scientific names, with some variations of spelling, have been used for the blue ling. Some of the references to these names are: *Molva byrkelange* (Walbaum, 1792)

Contribution given in honour of Gunnar Rollefsen at his 70th birthday.

by Fraser-Brunner and Palmer (1951), Kotthaus and Krefft (1957), Rahardjo (1961), Templeman and Squires (1962), Nielsen (1963) and Netzel and Stanek (1966). On the other hand, Svetovidov (1948) and Tåning (1958) have used *Molva dipterygia* (Pennant, 1784) and Kotthaus and Krefft (1967) *Molva dypterygia* (Pennant, 1784).

Strøm (1765) in Danish and (1767) for the same paper in German introduced a recognizable description and figure for the blue ling referring to the common name "Byrkelange". The paragraph from Strøm (1767) containing this description is quoted below:

"Dem Lysing (Gadus Merluccius) ist er in gewissen Stücken, nämlich in Ansehung des Unterkinnes, und der Beschaffenheit des Fadens unter der Kehle, zwar am ähnlichsten; hingegen aber ist er von demselben, in Betrachtung der Anzahl der Strahlen in den Finnen oder Flossfedern, und anderer Eigenschaften, so in der Beschreibung von Sundmöer bereits angeführt worden, und daher nicht nöthig hier zu wiederholen, doch zu unterscheiden. Da aber Linnaeus in Syst. Nat. Edit. 10 p. 254, den Lysing Gadus dipterygius, cirratus, maxilla inferiore longiore nennt, und diese Beschreibung sich eben sowohl vor den Byrkelange schickt, so kann ich nicht besser unterscheiden, als wenn ich den letztern so nenne: Gadus dipterygius, cirratus, maxilla inferiore longiore, pinna ani ossiculorum 70."

Müller (1776) refers to the blue ling and I quote below three of his entries of which no. 346 refers to the blue ling:

"345. G. *Mustela* dipterygius cirratus cirris quinque, pinna dorsali priore exoleta. D. *Kroll-Qvabbe*, *Moer-Qvabbe*, N. *Rødbrune Tang-Brosme*.

346. G. dipterygius, cirratus, maxilla inferiore longiore, pinnis analibus LXX. N. *Byrke-Lange* Str. S. 275. Act. nidr. 3, 446 t. 8. Aph. 1, 494.

347. G. *Aeglefinus* tripterygius cirratus albicans, cauda biloba, maxilla superiore longiore. D. *Kuller* N. *Kollie*, *Hyse*. I. *Ise*. Isl. R. 528 t. 26. Aph. 4, 537."

The use of "Byrke-Lange" by Müller is quite definitely as a common name. He lists it in his index of Danish and Norwegian vernacular names.

Pennant (1784) says: "Among the fishes which have hitherto shunned our shores are the Raia Clavata, Müller no. 309;...*Squalus Spinax*, 312; ...*Chimera Monstrosa*, 320, a most singular fish; ...*Gadus Brosme*, 341; *G. Dypterygius*, or *Byrke-lange*, 346; ...

Thus Strøm (1765, 1767) produced a description, figure, genus, common name and location that are sufficient to recognize the species in comparison with other lings, Müller (1776) quoted Strøm, and Pennant (1784) gave Müller as his reference.

Müller italicizes his specific but not his generic names and begins his specific names with a capital letter, but his "dipterygius" of G. dipterygius is not italicized and does not begin with a capital. It is

evident that the "dipterygius" of Strøm as used in referring to "Byrkelange", the blue ling, is the same word he has used immediately above in his description of the hake (Lysing) and consequently is descriptive, meaning two-finned (dorsal) in the same way that the next word "cirratus" and the phrases following are descriptive.

Similarly in Müller's account "G. *Mustela* dipterygius, G. *Aeglefinus* tripterygius, G. dipterygius", it is evident that the dipterygius (two-finned) and tripterygius (three-finned) are descriptive and that because also it is not italicized nor does the dipterygius begin with a capital, dipterygius is not presented as a species name.

Apart from his slip in naming the blue ling, Müller (1776) is consistently binominal and his names are recognized. Pennant's (1784, p. 76) fish names are quoted from Müller's binominal list, and in addition the blue ling scientific name is made binominal. It is my conclusion that Pennant's name can be accepted both on the basis of the rules set down by International Commission on Zoological Nomenclature (1964), Article 11C, and on the basis also that Pennant's reference to Müller fulfils the requirements of Article 16(a) as a valid indication.

Since the word dipterygius as used by Strøm (1765, 1767) and Müller (1776) is descriptive and not specific, Pennant (1884), who first set up the name as a scientific name *Gadus Dypterygius*, was perfectly at liberty to use the species term *Dypterygius* instead of the descriptive word dipterygius. Fleming (1828, p. 192) introduced the genus *Molva* (type *Gadus molva* L.) for the ling group. I conclude, therefore, that the scientific name of the blue ling is *Molva dypterygia* (Pennant, 1784).

MORPHOMETRIC AND MERISTIC CHARACTERS

The morphometric and meristic characters of the north-west Atlantic specimens (Tables 1, 2) are usually within or occasionally overlapping the range of *Molva dypterygia* from the north-east Atlantic. (Compare Svetovidov 1948, Fraser-Brunner and Palmer 1951, Templeman and Squires 1962, Rahardjo 1961, Nielsen 1963, allowing for the fact that Svetovidov's and Nielsen's body proportions of this species are based on the total length. See later.) The pelvic fin ending anterior to the posterior end of the pectoral separates them from *M. macrophthalma* (Rafinesque). The ratios of the length of the 1st dorsal base in 2nd dorsal base (6.5–7.4) are intermediate between and separate from those of *M. molva* (3.5–4.5) and *M. macrophthalma* (9.2–11.0) but are included in the range of this ratio for *M. dypterygia* of the north-east Atlantic (5.3–7.5).

The least height of the caudal peduncle is similar to that of *M. dypterygia* of the north-east Atlantic and lower than that of *M. molva*.

Table 1. Morphometric characteristics of the blue ling, *Molva dypterygia*, from the north-west Atlantic. (S.L. = standard length, H.L. = head length. Otherwise all percentages are of standard length. Apart from the total length occasionally measured fresh at sea, all other measurements were taken in the condition on examination, item No. 43.)

Item	Body character	No. 1 Dana Bank, W Greenland, 17 Aug. 1965	No. 2 Fylla Bank, W Greenland, 14 Aug. 1965	No. 3 Hermitage Bay, Nfld., 17 Sept. 1959. Templeman and Squires (1962)	No. 4 SE slope Grand Bank, 24 Nov. 1964
1	Total length: sea, fresh, mm[1]	777.0	858.0	1150.0	—
2	Total length: shore, mm[1]	—	847.0	1121.0	1241.0
3	Standard length: snout—end hypural, mm	723.0	783.0	1047.0	1152.0
4	Head length: snout—end bony operculum, mm	147.2	160.0	235.0	250.8
5	Head length: snout—end bony operculum, %	20.4	20.4	22.4	21.8
6	Snout length, % S.L.	6.4	6.6	6.9	7.1
7	Snout length, % H.L.	30.9	32.2	32.1	33.3
8	Orbit: horizontal diameter, % S.L.	5.3	4.5	4.9	4.9
9	Orbit: horizontal diameter, % H.L.	25.8	22.1	21.7	22.4
10	Orbit: vertical diameter, % S.L.	4.1	3.5	4.3	4.1
11	Orbit: vertical diameter, % H.L.	20.4	17.0	19.1	19.0
12	Cornea: horizontal diameter, % S.L.	3.7	3.6	ca. 3.4	4.2
13	Cornea: horizontal diameter, % H.L.	18.3	17.5	ca. 15.3	19.3
14	Interorbital: width, least fleshy, % S.L.	2.8	2.6	2.8	—
15	Interorbital: width, least fleshy, % H.L.	13.8	12.5	12.3	—
16	Interorbital: width, least bony, % S.L.	1.7	1.6	2.0	1.9
17	Interorbital: width, least bony, % H.L.	8.2	7.9	8.9	8.6
18	Post-orbital length: to end bony operculum, % S.L.	9.2	9.3	9.2	9.2

[1] Anterior tip lower jaw, with mouth closed, to post. end of caudal fin.

Table 1 (continued).

Item	Body character	No. 1 Dana Bank, W Greenland, 17 Aug. 1965	No. 2 Fylla Bank, W Greenland, 14 Aug. 1965	No. 3 Hermitage Bay, Nfld., 17 Sept. 1959. Templeman and Squires (1962)	No. 4 SE slope Grand Bank, 24 Nov. 1964
19	Post-orbital length: to end bony operculum, % H.L.	44.7	45.4	42.6	43.1
20	Lower jaw: protrusion beyond upper, % S.L.	0.7	0.6	0.5	0.9
21	Lower jaw: protrusion beyond upper, % H.L.	3.4	2.8	2.1	4.0
22	Barbel: length, % S.L.	1.9	2.2	0[2]	[3]
23	Barbel: length, % H.L.	9.5	10.8	0[2]	[3]
24	Body: greatest height, %	12.1	12.3	ca. 10.9	18.7
25	Caudal peduncle: least height, %	2.6	3.0	—	2.6
26	Snout—ant. base 1st dorsal, %	27.7	28.8	28.7	29.4
27	Snout—ant. base anal, %	45.2	46.0	47.5	48.8
28	1st dorsal base: length, %	7.5	7.9	7.8	8.2
29	2nd dorsal base: length, %	55.5	55.4	51.7	52.8
30	1st dorsal: greatest height, %[4]	7.9	8.4	8.4	7.6
31	2nd dorsal: greatest height, %[4]	5.7	6.1	6.1	5.7
32	Tip pelvic anterior to vertical from posterior end pectoral, %	3.7	4.1	5.6	6.5
33	Interorbital width, least fleshy, in length of head	7.3	8.0	8.1	—
34	First dorsal base in 2nd dorsal	7.4	7.1	6.6	6.5

[2] Absent, only a stub present.
[3] Unsuitable for measurement.
[4] Longest fin ray.

Table 1 (continued).

Item	Body character	No. 1 Dana Bank, W Greenland, 17 Aug. 1965	No. 2 Fylla Bank, W Greenland, 14 Aug. 1965	No. 3 Hermitage Bay, Nfld., 17 Sept. 1959. Templeman and Squires (1962)	No. 4 SE slope Grand Bank, 24 Nov. 1964
35	Height 2nd dorsal in height 1st dorsal	1.4	1.4	1.4	1.3
36	Sex	♀	♀	♀	♀
37	Sexual maturity	Imm.	Imm.	Mat. (spent)	Mat.
38	Ovary weight, kg	—	—	—	0.94
39	Egg diameter, mm	[5]	[5]	—	0.5
40	Round weight, sea, kg	1.41	2.36	—	—
41	Round weight on examination, kg	1.36[6]	2.18	3.8	9.9
42	Gutted and gilled weight, after examination, kg	—	1.96	—	7.1
43	Condition on examination	Excellent, measured fresh 1–1½ hr after capture	Good, fresh after freezing on ship and thawing in ice	Good, ex 10% formalin	Good, fresh after freezing on ship and thawing in ice

[5] Eggs not visible to naked eye.

[6] Weight on shore after freezing on ship, and thawing in ice on shore.

Table 2. Meristic characters of the blue ling, *Molva dypterygia*, from the northwest Atlantic.

Body character	1	2	3	4	5[1]	6[2]	7[3]
1st dorsal rays, No.	12	13	12	13	13	14	12
2nd dorsal rays, No.[4]	76	77	73	78	76	78	72
Anal rays, No.[4]	74	76	68	74	73	74	69
Pectoral rays, No.	19	20	20	21	19	20	18, 20
Pelvic rays, No.	6	6	6	6	6	7	7, 6
Vertebrae, No.	79[5]	78[5]	77[5]	79[5]	—	77	75

1–4, author, from St. John's Station specimens. Numbers from Table 1.

[1] Off S Labrador, February 1965 (Netzel and Stanek 1966).

[2] Off outermost islands near Narssalik, Frederikshaab District, SW Greenland, September 1928 (Jensen 1948).

[3] Near Narssak, Julianehaab District, SW Greenland, 1939 (Jensen 1948).

[4] In my counts all rays counted, i.e. last two rays counted as two.

[5] Including urostylar half-vertebra as one vertebra.

The relative head length (20.4–22.4 S.L.), the predorsal length (27.7–29.4 S.L.), and the preanal length (45.2–48.8 S.L.) of the four western Atlantic blue ling are considerably greater than those of blue ling from the eastern Atlantic in Nielsen (1963). These measurements of Nielsen attributed to standard length, are, however, taken from Svetovidov (1948) and are based on total length. When Svetovidov's measurements are adjusted upward for a standard length of 92.9% of total length (average of the four western Atlantic specimens in Table 1) the relative length ranges for the eastern Atlantic specimens become: for the head length (18.5–19.0 S.L.), for the predorsal length (25.5–27.2 S.L.), and for the preanal (40.8–47.6 S.L.). These eastern Atlantic ranges are close to or overlapping with those of the western Atlantic but the head and the predorsal (a large part of which is the head) measurements are still somewhat greater for the western Atlantic. Svetovidov's ranges are presumably for blue ling from the north-eastern Atlantic and the western Atlantic blue ling are presumably related to those of Iceland. Icelandic blue ling have higher meristic counts than those of northern Norway (Rahardjo 1961) suggesting lower temperatures and the possibility of slower growth rate and consequently a larger head at Iceland than in northern Norway.

In meristic characters, the number of 1st dorsal rays (12–14) is within the range of *M. dypterygia* of the eastern Atlantic (11–15), higher than that of *M. macrophthalma* (10–11, rarely 12) and lower than that of *M. molva* (13–16). The number of 2nd dorsal rays (72–78) is within the range of the eastern Atlantic *M. dypterygia* (69–83) and of *M. macrophthalma*

(74–82) but higher than that of *M. molva* (57–70). Anal ray count (68–76) is within the range of eastern Atlantic *M. dypterygia* (62–81) and that of *M. macrophthalma* (70–79) and higher than that of *M. molva* (55–67).

Vertebral number (75–79) is within the range of eastern Atlantic *M. dypterygia* (72–79), but higher than that of *M. molva* (62–67) and below that of *M. macrophthalma* (80–84). The number of pectoral rays (18–21) overlaps with that of *M. dypterygia* from the eastern Atlantic (18–20), is the same as that of *M. molva* and is higher than that of *M. macrophthalma* (15–18).

The meristic counts of the western Atlantic blue ling are high on the average and, apart from those of the 1st dorsal, are higher than the Icelandic averages which in turn are higher than those for the north-east Atlantic (Rahardjo 1961).

DISTRIBUTION

Records from scientists, and research and exploratory vessels

These records (Fig. 1, 2, Table 3) show a distribution of the blue ling from 66° 32′ N, ICNAF (International Commission for the Northwest Atlantic Fisheries) Division 1B, southward along the west coast of Greenland to ca. 60° 56′ N, Division 1F (see Fig. 2 for ICNAF area, Subareas 1–5 and divisions). There are no records for the Labrador subarea, ICNAF Subarea 2, three records from Subarea 3 and none south of this point, the most southerly record being at 43° 35′ N, Division 3N.

These records represent all the published and unpublished records of blue ling from the Canadian and West German research vessels.

A few of these are documented for meristic and morphometric characteristics (Table 1). Also, the blue ling is so different in appearance from the common ling that no errors in separation should be made by scientists and the European scientists are familiar with both species. Only one specimen of the common ling, *Molva molva*, has been reported in published records from the western Atlantic (from Subarea 3, Templeman and Fleming 1954). Also, Mr. Erling Bratberg (letter, 13 March 1969) says that he observed one common ling caught by a Norwegian research vessel on bottom longline in West Greenland waters several years ago, but that no other data are available regarding this capture. He also says that blue ling have not been observed on Norwegian research vessel cruises to the ICNAF area.

The two ling from West Greenland, reported by Jensen (1948) as the common ling, *Molva molva*, were actually blue ling, *Molva dypterygia* (Tåning 1958; Table 2). Canadian fisheries research vessels which have fished in all ICNAF subareas and for twenty years in Subareas 2–4 and

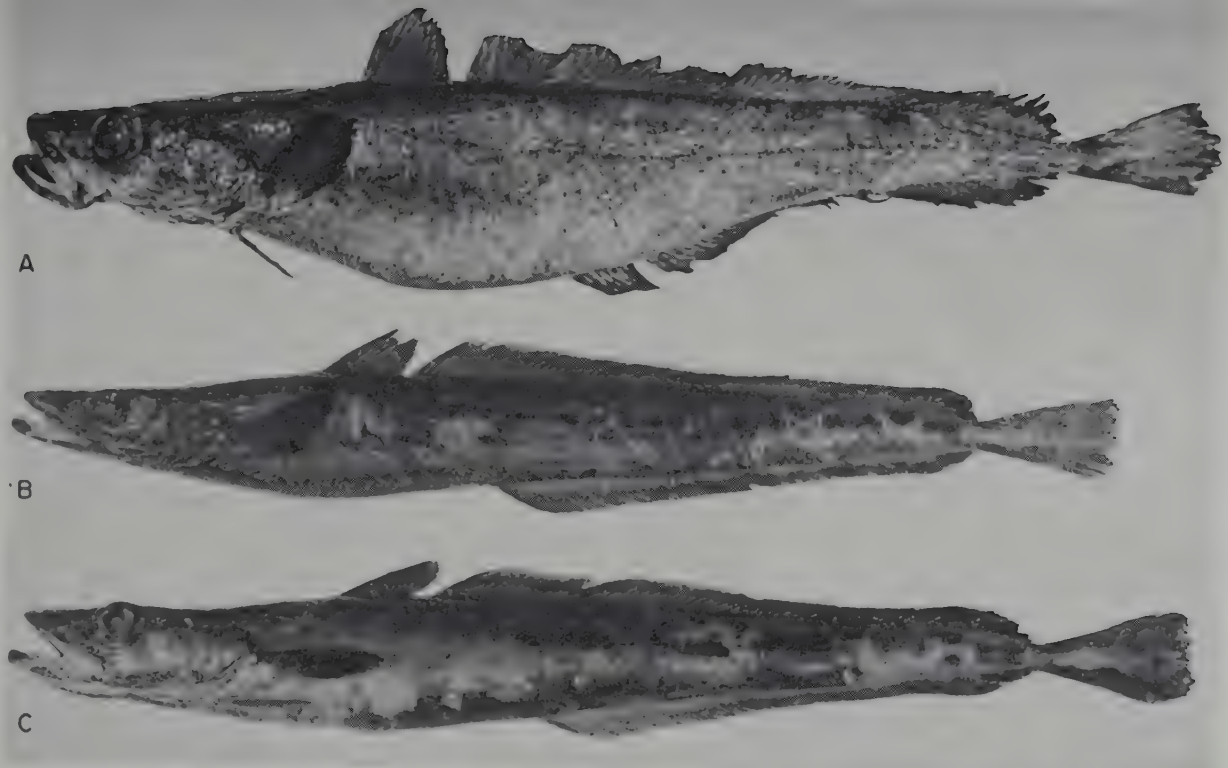

Fig. 1. Blue ling, *Molva dypterygia:* A, 1241 mm in total length, from the SE slope of the Grand Bank, November 1964, Table 1, No. 4, B, 858 mm in total length, from Fylla Bank, W Greenland, August 1965, Table 1, No. 2; C, 777 mm in total length, from Dana Bank; W Greenland, August 1965, Table 1, No. 1.

Table 3. Records of the blue ling, *Molva dypterygia*, from scientists and research vessels in the ICNAF area.

ICNAF div.	Year	Month	Position		Depth (m)	Bottom temp. (C)	No. fish	Length (cm)	Observer or reporter, ship, etc.
			N lat.	W long.					
1B	1967	27 Oct.	66° 32′	56° 25′	285–300	3.8	2	79, 86	*Walther Herwig*, J. Messtorff.
1C	1955	28 Sept.	65° 05′	54° 45′	250–300	—	1	77 ♂	Kotthaus and Krefft (1957). *Anton Dohrn*, A. Meyer.
1C	1965	25 July	64° 42′	54° 33′	260	4.6	1	1	*Anton Dohrn*, H. H. Reinsch.
1C	1965	25 July	64° 37′	54° 28′	260	4.6	6	—	*Anton Dohrn*, H. H. Reinsch.
1C	1965	25 July	64° 30′	54° 25′	260	—	1	—	*Anton Dohrn*, H. H. Reinsch.
1C	1965	24 July	64° 18′	54° 08′	220	4.6	1	—	*Anton Dohrn*, H. H. Reinsch.
1D	1959	3 Jan.	64° 10′	53° 33′	270	—	1	—	Trawler *Island*, explor. cruise, H. Koops.
1D	1965	14 Aug.	63° 34′	53° 00′	455–485	5.61	2	86, ca. 115[1]	*A. T. Cameron*, longline, author.
1D	1965	17 Aug.	62° 45′	51° 50′	385–395	5.3	1	78	*A. T. Cameron*, longline, author.
1D	1967	2 Nov.	62° 58′	52° 14′	300–315	5.1	6	70–90	*Walther Herwig*, J. Messtorff.
1D, 1E	1959	30 Apr.–15 May	ca. 62°	ca. 51°	—	—	ca. 50	—	Joensen (1960). Faroese otter trawler *Skalaberg* with research personnel on board.
1E	1928	Sept.	ca. 61° 38′	ca. 49° 25′	0	—	1	108	Jensen (1948). Reported as *Molva molva*.

[1] Floated away from close to ship. Observed by author.

Table 3 (continued).

ICNAF div.	Year	Month	Postion		Depth (m)	Bottom temp. (C)	No. fish	Length (cm)	Observer or reporter, ship, etc.
			N lat.	W long.					
1F	1939		ca. 60° 56′	ca. 46° 04′	—	—	1	133	Jensen (1948). Reported as *Molva molva*.
3K	1965	5 Feb.	52° 10′	55° 00′	236–260	—	1	99	Netzel and Stanek (1966). *Feniks* (Polish factory trawler).
3N	1964	24 Nov.	43° 35′	48° 50′	510–550	3.84	1	124	*A. T. Cameron*, E. J. Sandeman.
3Ps	1959	17 Sept.	47° 33′	56° 06′	240	—	1	115	Nfld. otter trawler *Pennyworth*.

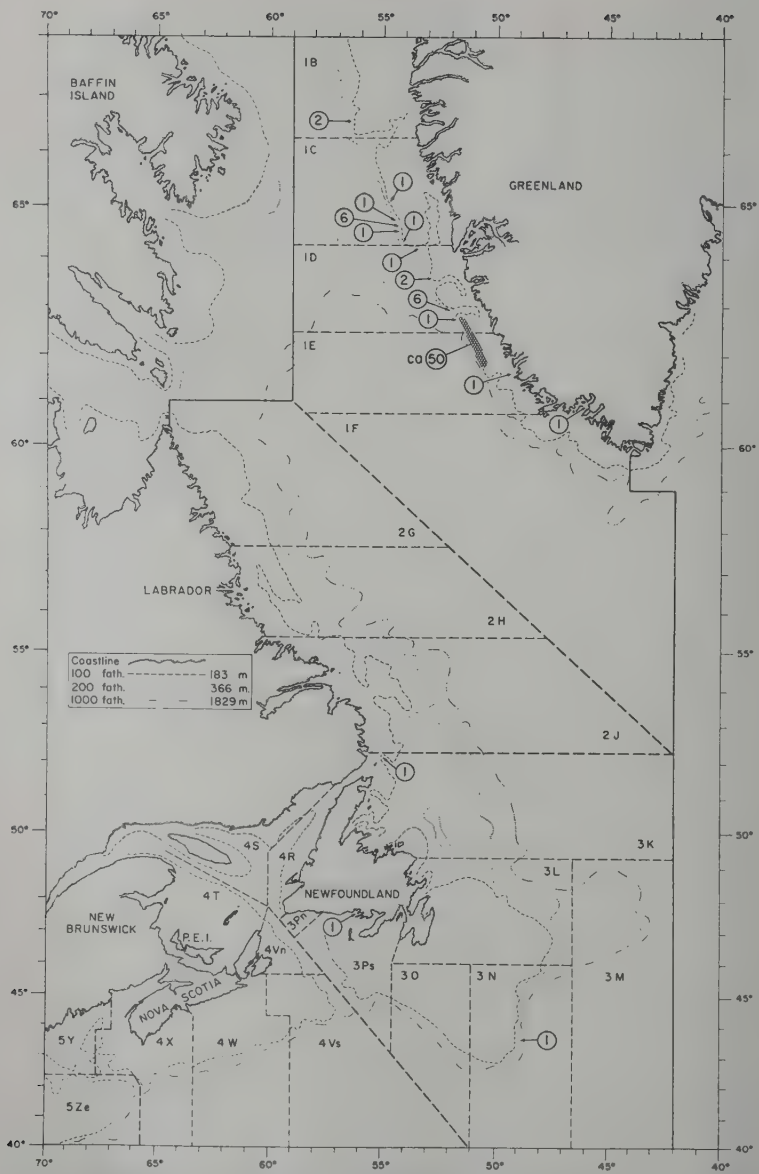

Fig. 2. Distribution of the blue ling, *Molva dypterygia*, as recorded from the ICNAF area by scientists.

for over half this period down to 730 m have never caught a common ling. Dr. J. Messtorff has informed me (June 1968) that research vessels of the Federal Republic of Germany have never caught a common ling in the ICNAF area although a number of blue ling were captured (Table 3).

Serebryakov (1965) reported four eggs of *Molva molva* from the Scotian Shelf portion of Subarea 4 from Soviet ichthyoplankton collections in 1959–1962. I am not certain whether or not eggs of blue ling can be distinguished from eggs of common ling and if so at what stages.

The blue ling are usually reported from deep water, 220–485 m, in West Greenland and 236–550 m in the Newfoundland area but one of the West Greenland fish reported by Jensen (1948) was harpooned at the surface near shore. Temperatures for the deep water catches were between 3.8 and 5.6 C (Table 3).

Although only the blue ling in Table 3 have been reported by scientists, and only the smaller number of Tables 1 and 2 further authenticated by morphometric and meristic characters, much larger quantities of ling and blue ling have been reported in commercial statistics from the ICNAF area.

The ICNAF Statistical Bulletins, 1955–1967, indicate (Table 4) small commercial landings of ling, *M. molva*, usually from Subarea 1 (West Greenland) but also from Subarea 2 (Labrador) and Subarea 3 (the Newfoundland area).

At my request, Dr. B. J. Kowalewski of ICNAF has supplied the ling catch records in all the national submissions of fisheries statistics to ICNAF

Table 4. Landings of ling (metric tons) from ICNAF subareas (as published in ICNAF Statistical Bulletins after screening out probable errors. Ling always defined in ICNAF list of species as *Molva molva* (L.)).

Year	ICNAF Subareas					Total 1–5
	1	2	3	4	5	
1954	2	0	0	0	0	2
1955	18	0	0	0	0	18
1956	2	0	0	0	0	2
1957	6	0	0	0	0	6
1958	0	22	0	0	0	22
1959	0	0	0	0	0	0
1960	5	0	4	0	0	9
1961	3	0	1	0	0	4
1962	1	0	0	0	0	1
1963	4	1	0	0	0	5
1964	0	0	0	0	0	0
1965	0	0	10	0	0	10

since 1952. The result is Table 5 which is not very much different from the published records (Table 4) except for the considerably larger landings in 1964. All the ling except the small amount caught by the Faroese fishermen (which was caught by longline) were taken by otter trawl in redfish, cod or mixed cod and redfish fishing.

There are seventy-four records of ling, *M. dypterygia*, from West Greenland by scientists, and apart from BRATBERG's sight observation of a single specimen, *M. molva* has not been recorded from this area. Although in my cruise in West Greenland in July–August 1965 on the *A. T. Cameron*, three blue ling were taken among the small number of fish caught by longline, in about twenty years of groundfish dragging by the *Investigator II* since 1946 and by the *A. T. Cameron* since 1958, in Subareas 2, 3 and 4 at depths in many cruises to 730 m, no ling have been caught by the *Investigator II* and only one by the *A. T. Cameron*. Ling are thus apparently very rare in Subareas 2 and 3, no records of *M. dypterygia* having been reported by scientists from Subarea 2 and only three specimens from Subarea 3.

The larger landings of 1964 (Table 5) from Subareas 1 to 3 and the small landings from Subarea 4 were all reported by Germany except for three tons by the United Kingdom in Subarea 1. Moreover Germany reported 259 tons as blue ling and the remaining 26 tons as ling. Also the one ton of ling caught by Germany (the remaining five tons were landed by Iceland) in Subarea 1 in 1957 and the two tons caught by Germany in Subarea 1 in 1959 were reported as blue ling. All the remaining catches were reported as ling with no indication of separation into common ling or blue ling except that ling was designated in the ICNAF list of species as *Molva molva* and ling is the European name (in English) for *Molva molva*. Dr. ARNO MEYER, in his letter of 26 February 1968, says that *Molva molva* is always reported in German statistics as ling and *Molva dypterygia* as blue ling.

The 601 tons of ling from Subarea 5 (Gulf of Maine-Georges Bank) in 1964 (Table 5) were reported by Poland and must refer to one or both of the hakes, *Urophycis chuss* or *Urophycis tenuis*. Ling is one of the common names for these hakes in eastern Canada and eastern United States.

After the ICNAF Statistical Bulletin for 1963 (1965) the ling, *Molva molva* (L.), was deleted from the list of common and scientific names used in the Statistical Bulletin.

Although the relatively large quantities of ling caught by Poland in Subarea 5 in 1964 (Table 5) were presumably hake, it is not possible to explain the reported landings of ling from Subareas 2 and 3 in this way. The total landings from Subareas 2 and 3 between 1958 and 1966 are in metric tons from ICNAF Divisions 2G(1), 2H(12), 2J(47), 3K(33),

Table 5. Landings of ling from the ICNAF area (metric tons round fresh. Original data as reported to ICNAF).

Year	ICNAF subareas					
	1	2	3	4	5	Total
1953	Ø (Iceland)	—	—	—	—	Ø
1954	—	—	—	—	—	—
1955	14 (Iceland 14, Germany Ø)	—	—	—	—	14
1956	1 (Germany)	—	—	—	—	1
1957	6 (Iceland 5, Germany 1[1])	—	—	—	—	6
1958	—	22 (Germany)	Ø (Germany)	—	—	22
1959	2 (Germany)[2]	—	—	—	—	2
1960	5 (UK 1, Germany 1, Iceland 3)	—	4 (Iceland)	—	—	9
1961	3 (Germany)	—	1 (Germany)	—	—	4
1962	1 (UK 1, Germany Ø)	—	—	—	—	1
1963	4 (Germany 3, UK 1)	1 (UK)	—	—	—	5
1964	220 (Germany 217[3], UK 3)	37 (Germany)[4]	28 (Germany)[5]	Ø (Germany Division 4W)[6]	601 (Poland)	886
1965	1 (Denmark (Faroes))	—	12 (Iceland 9, Denmark (Faroes) 2, UK 1)	—	—	13
1966	4 (Denmark (Faroes) 2, UK 2)	—	—	—	—	4

[1] Blue ling.
[2] Blue ling only.
[3] Blue ling plus ling—197 tons of blue ling included.
[4] 35 tons of blue ling included.
[5] 27 tons of blue ling included.
[6] Ling plus blue ling.
Ø Magnitude more than zero but less than ½ ton.

3L(1), 3M(5), 3P (less than 0.5) and Subarea 3, Division unknown (6). Thus the reported landings are from Subarea 2 and mainly the northern sections of Subarea 3. Of these ICNAF divisions, only 3P possesses any but rare specimens of hake. The only fish in Subarea 2 at all hake-like and which occurs in modest numbers in the deep water is the small blue hake, *Antimora rostrata*, which is presumably unlikely to be called ling. In any case 52 tons of these ling from Subareas 2 and 3 are reported by Germany in 1964 as blue ling which shows that it is not hake that is being reported.

Dr. Arno Meyer has written me (26 February 1968) that the German blue ling statistics reported to ICNAF for 1964 are incorrect. These blue ling reported by West-German vessels were caught off East Greenland and were referred to the ICNAF area by wrong assignments of areas when splitting mixed trips, mainly of cod and redfish, which were caught in the different areas on the same trip.

For Subarea 1 (West Greenland), neglecting the incorrect West-German records for 1964, in the years from 1955 to 1966 where records are available for the divisions of Subarea 1, the following total landings of ling (occasionally reported as blue ling) are reported (in metric tons): 1A(0), 1B($<\frac{1}{2}$ ton), 1C(2), 1D(3), 1E(2), 1F(11). If the monthly records of $<\frac{1}{2}$ ton are equated as $\frac{1}{4}$ ton each the landings from these divisions become: 1A(0), 1B($\frac{1}{4}$), 1C($2\frac{1}{4}$), 1D($5\frac{3}{4}$), 1E($3\frac{3}{4}$), 1F(12). It is apparent that most landings come from the southern divisions of Subarea 1 where deep-water fishing is carried out for cod and redfish. Although some of the ling statistics from Subarea 1 may still be incorrect assignments from mixed landings from East and West Greenland, the quantities and locations appear to be reasonable and possible.

It is presumed that all ICNAF landings of blue or common ling reported from Subareas 2 and 3 are falsely assigned in the same way from the landings of vessels which had fished East and West Greenland waters. Some of the very small catches of one to several tons of blue ling in West Greenland are presumably local catches in this area, but there is no certainty that they are always correctly allotted between the divisions of Subarea 1, as assignment of ling, pro rata with landed catches of cod and redfish, may spread the blue ling into more divisions and may also divide some East Greenland blue ling among the West Greenland divisions.

CONCLUSION

From the data presented, it is concluded that, apart from rare specimens, the common ling, *Molva molva*, is not present in the ICNAF area.

The blue ling is scarce but not rare in West Greenland but is rare in areas south of West Greenland, the most southern records being from ICNAF Subarea 3.

SUMMARY

1. A discussion of the various scientific names used for the blue ling leads to the conclusion that the correct name is *Molva dypterygia* (Pennant, 1784).
2. Meristic and morphometric characteristics are provided for two blue ling from West Greenland and one from the Newfoundland area.
3. The morphometric and meristic characters of blue ling from the north-west Atlantic specimens are usually within, overlapping or close to the ranges of these characters for *Molva dypterygia* from the north-east Atlantic.
4. The commercial statistics for ling in the ICNAF area are discussed and attention called to some of the errors.
5. It is concluded that blue ling are present in small numbers in the West Greenland area and rare in the remaining areas, the most southern definite records being from ICNAF Subarea 3.

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I am very grateful to Dr. Arno Meyer, Dr. J. Messtorff and Dr. H. H. Reinsch of the Institut für Seefischerei, Hamburg for providing information on the distribution of the blue ling, to Mr. Erling Bratberg of the Fiskeridirektoratets Havforskningsinstitutt, Bergen for information on ling catches in the ICNAF area by Norwegian research vessels, and to Mr. E. J. Sandeman, scientist-in-charge of the *A. T. Cameron* when the second St. John's Station specimen of the blue ling from Subarea 3 was obtained. I am also grateful to Mr. L. R. Day and Dr. B. J. Kowalewski of the ICNAF staff at Dartmouth, Nova Scotia, who provided unpublished information on reported catches of ling in the ICNAF area.

I have consulted Mr. G. Palmer of the British Museum, Natural History on the correct scientific name for the blue ling and have benefited much from my correspondence with him on this subject.

Photographs are by Mr. E. L. Rowe.

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THE PLASTIC SEABED "OYSTER" FOR MEASURING BOTTOM CURRENTS

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Many of his friends will recall that Gunnar Rollefsen had a genius with simple materials—as witness his achievement in taking a cine-film of cod spawning with simple gear at a time when others possessing expensive apparatus had had but scant success.

The recollection has emboldened the present writer to submit for publication in the volume now honouring Rollefsen's seventieth birthday, a small paper which deals with the first employment of a device for measuring bottom currents whose very keynote is simplicity. It is not unreasonable to maintain that there are various problems in oceanographical research where a simple and cheap apparatus can have real merit on grounds other than those of economy and simplicity. Sometimes the use of such a device may be the only way of tackling a problem hopefully, and although that to be described does not produce a continuous record but makes only easily-repeatable single observations, these latter can be just what is wanted for certain purposes.

In what follows we shall give an account of a modest tool for investigating seabed currents, without depth limitation. The broad nature of the device can be conveyed at the outset by merely quoting the legend carried on a large diagram from which our present figures have been cut out. The legend in question reads:

> "This device is meant to be thrown out anywhere from any kind of ship over any ocean depths. It is designed to sink to bottom to make a single record of bed current speed and direction. Some time later it will rise to surface to travel as does a drift bottle until cast ashore. It carries a multi-language questionnaire paper, the perusal of which should result in the investigator receiving back by post the directional pendulum bearing permanent interpretable grooves."

Contribution given in honour of Gunnar Rollefsen at his 70th birthday.

Any serious paper dealing with current measuring would of course be expected to make many citations from the nigh-staggering literature which now exists, and any writer on bottom currents would equally be expected to quote from the many papers which give the results of effort spent to measure them. Because there is (not surprisingly!) a real paucity of data on currents right down on the deep ocean bed, and because much of what is known about them has come from photographic studies of their effects of various kinds, we can here justifiably abstain from citations on the grounds that we have attempted a novel approach. We were concerned to produce a device which would not require the possession and operation of deep sea cameras, would involve only very modest expenditure of money, would not call for the availability of a specialist ship, could be used more or less anywhere without any concern at all for weather, and would require no line attachments at all to an attendant ship or to a mooring. Because our aim was to measure actual bed currents there would be no similarity with the well-known seabed drifter.

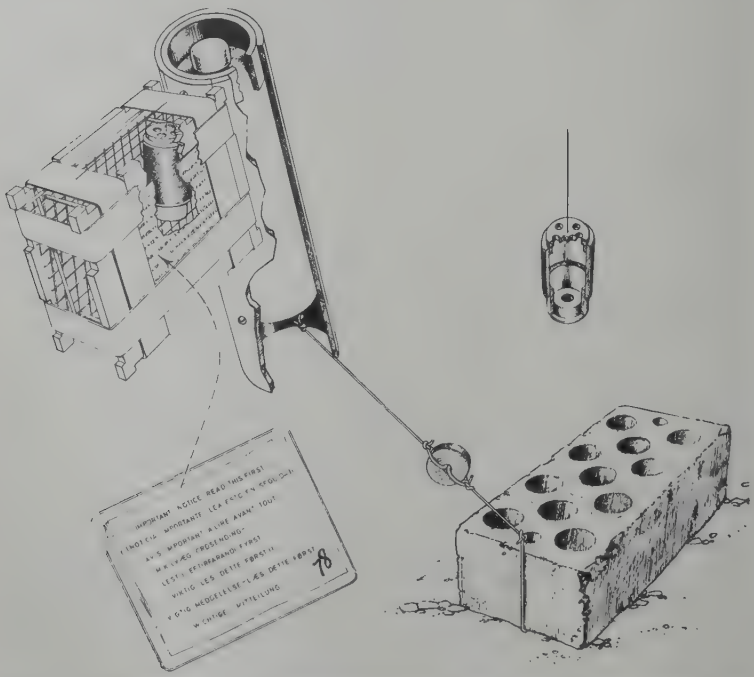
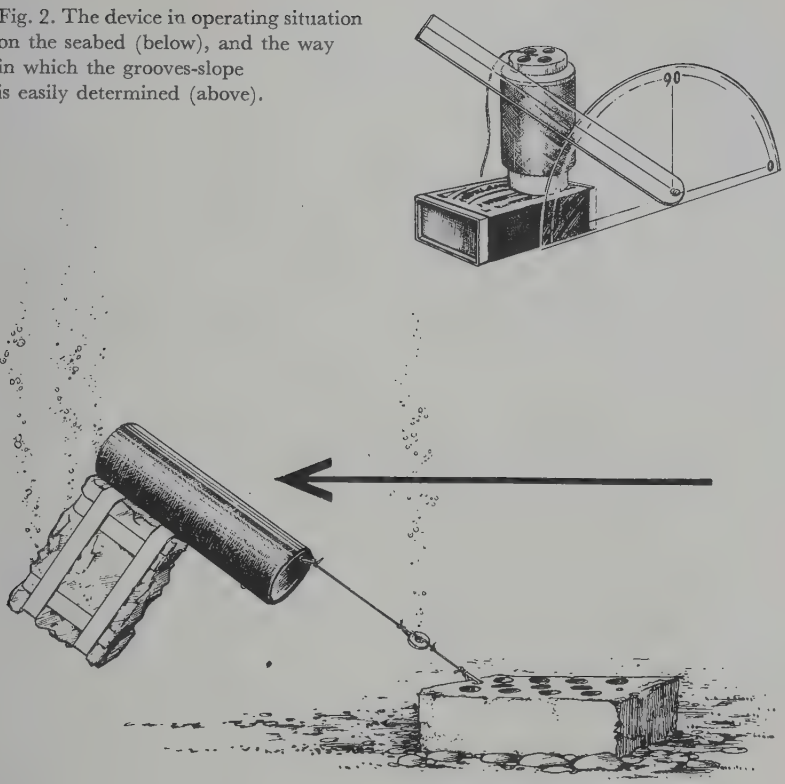


Fig. 1. The construction of the device as described in the text. The suspended directional pendulum is shown (in section) — as also is the come-loose tether to the brick.

Fig. 2. The device in operating situation on the seabed (below), and the way in which the grooves-slope is easily determined (above).



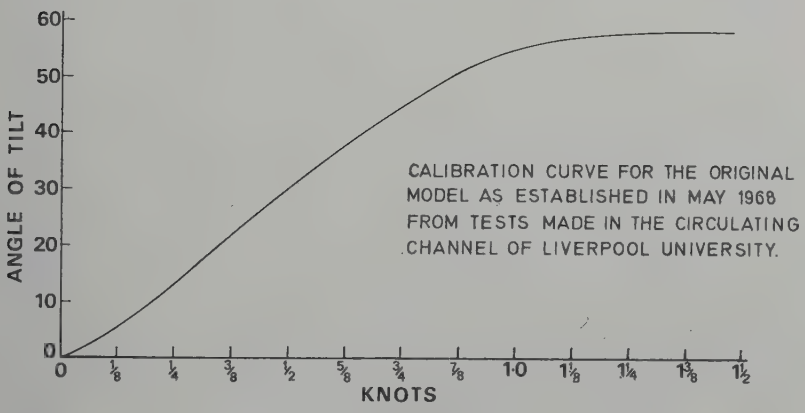


Fig. 3. Tilt/speed curve.

This paper can be kept brief and realistic if we do little more than reproduce (1) the memorandum which we sent to finders of the stranded "oysters" and (2) the diagram which we also posted to them. For publication purposes however, we have cut the large diagram into three illustrations, Figs. 1, 2, and 3.

We particularly wished to avoid the trouble of paying rewards, and we therefore relied upon the desire of finders to receive promised information about their finds proving sufficient to bring in returns. In the event it certainly did so, and some finders even asked that we should not bother to refund their postage costs.

A sufficient description of the "oysters" is afforded by reproducing the memorandum sent to finders—and we here give it as posted to the latest of these:

> *MEMORANDUM FOR THE INFORMATION OF PERSONS WHO HAVE FOUND ONE OF OUR "STRANGE OBJECTS" STRANDED AND HAVE KINDLY SENT BACK TO US THE PART ASKED FOR BY THE MULTI-LANGUAGE YELLOW PAPER WHICH THEY FOUND BOUND INTO IT.*

At the outset it is to be said that the object which you found relates to a new method of sea research which could be called: "Seabed Currents by Post" to use rather picturesque language. You will be best able to appreciate what is involved if you read what follows whilst looking at the artist's diagram now sent to you. It is convenient for workshop and stock purposes to have a nickname for various sorts of device when many exist—and the thing you found goes conveniently under the name: "Plastic Seabed Oyster". The use of the word "Oyster" will become obvious we think. The object which you found and which we shall call a "P.S.B.O." from now on, was originally tossed overboard from the survey launch *Waterwitch* (Lieut.-Cdr. J. Paisley, R.N. (retd.)) at a spot near Alderney in the Channel Islands on 23rd September, 1968. It was sent to the bottom in the depth of about 172 metres in a long deep trough in the seafloor called the Hurd Deep. This deep is of interest for a number of reasons, and in the old days masters of home-bound sailing ships liked to find it with their leadlines to assist their positioning. A number of the devices were thrown out each hour round the clock so that we could hope to learn what changes in speed and direction the bottom tidal streams might display in this area where they are strong (and known) on the surface. There would have been real difficulty in measuring the bottom currents in the wild weather which prevailed at the time, and the occasion was therefore very suitable for trying a new way of working which does not require a ship to keep an instrument captive on a suspension line. The following is a description of the P.S.B.O. as it was when

thrown out to sink to bottom. Two small rectangles of buoyant stiff polythene held about two inches apart by four strong perishable stiff rods (3.9 mm in diameter) set into little pits drilled in their corners on their inwards sides, were bound round with powerful stretched "garters" made of non-perishable butyl rubber. Extra strong bands of ordinary rubber were added to increase the squeeze force. These bands were disposed both across the length (14.5 cm) and the width (11.0 cm) of the polythene rectangles. The hold-apart rods were made of a corrodible alloy which fizzes away in sea water. On the inwards face of one of the polythene plates was fixed an equal-sized rectangle of green square-meshed plastic material such as is used for making meat safes etc. This material has stiff and pronounced raised ribs and the sheet of it used in the P.S.B.O. has these prominent hard ribs running parallel to the 14.5 cm edges of the plastic rectangle.

Hung midway between the polythene rectangles (at one end) is a cylindrical pendulum suspended on a terylene thread set into the centre of its top. This pendulum is about the size of a wine bottle cork. It is made from a polythene tube such as pharmacists use for keeping capsules in. The tube has holes in it to allow it to fill with water. Over the tube is a sleeve of soft rubber tubing and, over this latter, a strip of thin pure copper foil (0.7 mm thick) is wound to encompass the whole circumference of the tube. The copper foil is held secure from twisting movements by means of a thread tied suitably through it and the cylinder. The circular base of the pendulum contains a tight-fitting disc compass made from ceramic steel. This compass is very powerfully magnetized across its diameter which means that one point on the circumference seeks north, and the opposite one south. As so far described, if you held the cylindrical pendulum by the suspension thread, it would always rotate to come to rest in the same position. The suspension of the pendulum between the polythene rectangles is so arranged that it stays always midway between them so long as the hold-apart rods are intact. As so far described, if you tilted the plates the pendulum would remain vertical, but, if whilst you held them tilted the rods could suddenly crumble, the "oyster" would close with a powerful grip. The result would be that the plastic mesh would press its ribs into the copper and would make deep grooves in that soft covering of the directional pendulum. If you now forced the plates apart again and removed the pendulum, you would of course find that the grooves were on the slope—that is, not parallel to the top and bottom of the pendulum. These remarks explain how the grooves which you may have noticed on the pendulum which you returned to us were made.

Let us return to the device as so far described. The next step in its manufacture was to fasten the box affair comprising the two plates, the

hold-apart rods, the rubber binders and the pendulum—at right angles to the top of a short length of plastic tubing (6 cm wide and 26 cm long) containing a thin-skinned plastic detergent bottle filled with junk oil. This addition is made to give the gadget more buoyancy—more flotation power. From a point on the circumference of this tube (at its bottom) a string leads away which has to act as a limp tether. We next tie the free end of this string to a brick—using for convenience one of the holed kind of brick known to builders as "airbricks". We allow about 20 cm for the length of the limp tether. We next sink the whole affair in a glass tank of sea water. It "floats" of course but at first the box part rides up somewhat above the horizontal. We then wind some thick solder wire round the box at the end away from the tube until it (the box) is horizontal. If we could now set the sea water in motion (thereby imitating a current), the tube would incline from the vertical and the box would dip below the horizontal—but the directional pendulum would always hang vertical. Clearly, the faster the current the greater would be the angle of tilt. Thanks to suitable laboratory tests made in water moving at various known speeds, we know the connection between angle of tilt and speed of current. Obviously we want the current to tilt the whole device without "blowing" directly on the pendulum. We therefore enclose the box part within a close-fitting cellophane bag such as is used for packing sandwiches—but we put some holes in the top of the bag to allow the escape of air and of the gas which will be produced when the rods fizz away.

The way of using the devices is as follows: we take them in our ship to a place where the bottom currents are of interest to us. Then we toss them overboard separately with the tether of each tied to a brick—but, in the tether, we incorporate a washer of the same corrodible alloy as the rods are made of. This washer takes much longer to fizz away and crumble than the rods do. When the P.S.B.O. reaches the bottom, if there is a current it tilts of course. When the hold-apart rods crumble the oyster snaps to and squeezes the pendulum very tightly to produce grooves whose slope is in proportion with current speed, and whose position on the pendulum (when referred to the known north-seeking vertical of the latter) reveals the direction of the current. Some time after the answer has become securely squeezed within the P.S.B.O., the tether washer crumbles and lets the device rise to the sea surface. Thereafter it floats on and on much under wind influence until such time as it fetches up on a beach. This makes one think of drift bottles and of the thousands of records of their travels which we hold—but, with the P.S.B.O., we want the winds to blow them along so that we shall not have to wait so long for returns as we might in the case of drift bottles carefully ballasted to escape wind influence.

We do not of course care where the P.S.B.O.'s go ashore; it is all the same to us so long as we get returns from them—their message having been securely locked within them ever since they closed on the seabed.

One thing remains to be explained. Clearly we had to have a way of hearing from persons who might find P.S.B.O.'s stranded on beaches. Obviously we could not accept the expense of much printing on plastic even if space sufficed. We therefore had recourse to multi-language questionnaire sheets enclosed in heat-sealed wallets of clear thin polythene. We tested these latter in water pressurized to more than 1,400 kilograms per square metre which is a much greater pressure than exists anywhere in the deepest parts of the oceans.

After the P.S.B.O. which you found stranded had risen to the surface, it travelled up the whole length of the English Channel under the influence of currents and winds. It rounded Kent and travelled on along the coasts of Essex and Suffolk to reach Norfolk after accomplishing a journey of about 280 miles. At the time of writing this twenty-one of the forty P.S.B.O.s put out near Alderney have been found stranded on the Norfolk coast. It may well be that some not urged ashore there by the north-easterly winds then prevailing, may travel on to go ashore very much further afield.

The recipient of this memorandum is warmly thanked for his help, and is informed that he is completely free to make any use of the story he may wish.

Your number was:—

Your finding date was:—

Your bottom current was:—

Addendum.

Since the above was written, two further P.S.B.O.s have been returned —of which yours is one. That returned from near Saltburn on the northernmost part of the Yorkshire coast and also that from Whitley Bay in Northumberland have travelled on about 130 miles further than those returned from the Norfolk coast. In other words they have covered a track of about 410 miles from the place where they were put on the sea bed.

[Memorandum ends here]

The multi-language yellow questionnaire paper referred to in the foregoing memorandum brought very pleasing success indeed, and we became accustomed to the postman bringing neat little parcels with the two supplied adhesive labels affixed to them.

The wording of the questionnaire paper (folded to the size 11.5 cm by 9.0 cm) was as follows:

(*a*) The portion visible through the polythene envelope on recovery read thus:

IMPORTANT NOTICE – READ THIS FIRST !!

!! NOTICIA IMPORTANTE – LEA ESTO EN SEGUIDA !!

AVIS IMPORTANT – A LIRE AVANT TOUT

MIKILVÆG ORDSENDING –
LESTU EFTIRFARANDI FYRST

VIKTIG – LES DETTE FØRST !!

VIGTIG MEDDELELSE – LÆS DETTE FØRST

WICHTIGE MITTEILUNG !

(*b*) the subsequent wording was the following printed successively in English, Spanish, French, Icelandic, Norwegian, Danish, and German:

The strange object which you have found stranded, should contain within itself information relating to the speed and direction of the water movements on the deep ocean bed at a spot very far away and on an occasion perhaps very many months ago.

If you will very kindly help us by acting as requested in what follows, the whole story will be told to you by letter as soon as we hear from you.

We particularly need to receive from you the little polythene tube coated with thin copper foil which you should have found squeezed within the object which you discovered stranded. This should have marks upon it which we can interpret for our purposes, and we accordingly beg you to send it back to us wrapped in a way which will preserve those marks. You will find enclosed with this two small printed labels which become strongly adhesive when their brown paper covers have been removed. Please affix them both to the little parcel which we strongly hope you will send to us. One of them will save you the trouble of writing our address, and the other will let the British Customs know what is contained. Please tear out from this sheet this portion which is in your own language, and please post it back to us with the undisturbed tube after having filled in the little questionnaire beneath. If you have difficulties, please solicit the help of a local official—and please tell us whether you require the postage expenses to be refunded.

As time goes on we shall hope to give finders more information than that obtained from the single object found by them. Please tell us very clearly your own name and address, and please state where and when you found the stranded object.

Our address is:

The National Institute of Oceanography,
WORMLEY, GODALMING, SURREY, ENGLAND.

Your name: .....

Your address: .....

.....

Date of finding: .....

Place of finding: .....

Our identity number marked on the paper: .....

It is pleasing to be able to state that all the directional pendulums returned to us were in excellent condition and had been carefully packed. The "grooves in copper" method of recording had been chosen after much pondering how best to achieve a record which would be virtually indestructible by the handling the pendulum would get from finders, and which would stand up to much rough usage due to wave motions on beaches. The reader might wonder how the method would work miles deep when the rubber sleeve under the copper would be "bone hard" before the oyster closed. This was checked by tests in a pressure tank. It was expected and proved that once the oyster had closed tight upon hard rubber whilst down below, it would maintain its powerful grip and make the grooves as the rubber softened again on ascent to surface. When the oysters were put out in the Hurd Deep a violent storm was raging and the tides were top equinoctial springs. As already remarked, all the returned pendulums were easily interpretable and there is no reason at all to doubt any of the speed values which, "round the clock", ranged from slack to one-knot on bottom below the 172 metres of water. It is however unfortunate that the directions are not so credible from this first experiment. It is clear that the hung pendulums must have spun somewhat from touching the side plates during surgings of the oysters. This is a fault which has now been rectified in preparation for another experiment. The pendulums are now pivotted on a swinging bracket in such a way that they cannot touch the sides of the oysters before closure.

Oysters furnished with the new pivotted pendulum have had their behaviour effectively checked in the following way. Some of them adapted to close in ten minutes were put on bottom from a lightship moored in the estuary at Harwich. They were used both on the seagoing and land-going stream along with infallible current-measuring jelly bottles of the same timing. In all cases a complete direction check was obtained. It is now intended to use the oysters in the greatest depths of the Bay of Biscay. When this is done they will probably have been modified a little to increase their sensitivity still further at lowest speeds. It is easy enough to cater for very slow speeds and equally easy to cater for speeds up to and beyond three knots—but there are of course real problems in making an oyster which will be satisfactory for both. Ideas are not lacking but they are a matter for the future. We may conclude by expressing the hope that publicity given by the B.B.C. might help towards future success.

ACKNOWLEDGEMENTS

I am indebted to my colleague Mr. D. Bookham for all the constructional work involved, an to our artists Mr. N. R. Satchel and Miss P. E. Williamson for all the drawings.

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GROWTH OF SOCKEYE SALMON IN RELATION TO ABUNDANCE IN THE KVICHAK DISTRICT, BRISTOL BAY, ALASKA[1]

By

Ole A. Mathisen

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INTRODUCTION

Intensive exploitation of Bristol Bay sockeye salmon (*Oncorhynchus nerka*) by both domestic and high-seas fishing has spurred the effort to formulate rational management procedures. Regardless of approaches to the formulation, two elements are indispensable: an accurate forecast of the run of adult salmon and a reliable estimate of the escapement that will produce the largest return.

Sockeye salmon leave the Kvichak River for the sea either in the second year of life (age I smolts) or in the third year (age II smolts). Nearly all survivors from both groups return after two or three years in the sea; thus practically all of the total production from an escapement is realized in instalments of 4, 5, or 6 years after the year of spawning. (Other age groups are generally negligible in number.)

Ricker (1962) compiled the available data on ocean survival of smolts and average length at the time of seaward migration for both North American and Asian sockeye salmon stocks. Survival generally was highest for the stocks that produced the largest smolts; but within one river system survival was generally not related to size. Where there is cyclic variability in run magnitude, as in the Kvichak River stock, a new dimension is added. Since the progeny from a given year of spawning return 4, 5, and 6 years later, the cyclic pattern of salmon abundance would not persist if the survival rate of the progeny were not higher in the peak cycle year than in off cycle years. For the Kvichak stock, there is a return of more than three mature fish per spawner of the peak year class, but of only

[1] Contribution No. 292, College of Fisheries, University of Washington.

Contribution given in honour of Gunnar Rollefsen at his 70th birthday.

one or two mature fish per spawner of the off year classes or even less. On the other hand, smolts during the peak cycle year may be 10–20 per cent smaller in length on the average than smolts during the off cycle years.

The interactions between the strength of year classes of salmon, primary and secondary production in the nursery area, and abundance of predators and food competitors, which result in a cyclic run abundance in the Kvichak River, can best be studied by a simulation model. But if such a model shall be useful for predictive purposes it must be a realistic one and not only one of verisimilitude. In order to achieve this a number of functional relationships must be determined. The present paper represents an effort to this end by discussing some functional relationships between growth of salmon and population density in the Kvichak River system.

SMOLT SIZE IN RELATION TO MAGNITUDE OF PARENT ESCAPEMENT

It has been observed in many river systems in North America and in Kamchatka that an inverse relationship exists between the average size of smolts and population size (Krogius 1961, Johnson 1965, Burgner *et al.* 1969).

During the period 1953–1968, for which data are available on escapement and corresponding smolt abundance for the Kvichak stock, there were seven years in which less than one million fish escaped to the spawning grounds, three years in which escapements ranged from 2.5 to 3.7 million spawners, and three years in which escapements were exceptionally large. In 1956 the escapement numbered 9.4 million fish; in 1960, it was 14.6 million fish; and in 1965, it was 24.3 million spawners (Table 1). The total number of smolts produced increased over these last three cycle years, but the number of smolts produced per spawner declined. Nevertheless, it is informative to determine whether the average length of smolts has been a function of escapement size over the years.

The average lengths of age I smolts and age II smolts are plotted against the magnitudes of parent escapements in Fig. 1. In both cases, average length decreased as parent escapement increased until parent escapement reached a certain level, after which average length stabilized. For age I smolts this level was about four million spawners. Despite exceptionally large escapements in 1956, 1960, and 1965, the average length of age I smolts produced varied only from 82 to 86 mm. For age II smolts, the level at which the smolt length stabilized itself was about nine million fish. For the two largest escapements during the period under consideration, the average length of age II smolts was about 100 mm.

Table 1. Sockeye salmon escapements and average lengths of smolts produced, Kvichak River, 1952–1965.[1]

Year	Escapement, thousands	Average length of smolts, mm		Index catch of age I and II smolts, thousands
		Age I	Age II	
1952	5,970	—	109	—
1953	321	89	116	66
1954	241	92	120	39
1955	250	96	114	89
1956	9,443	84	99	6,045
1957	2,964	80	108	639
1958	535	91	117	72
1959	680	92	110	98
1960	14,630	82	98	5,247
1961	3,706	83	108	1,717
1962	2,581	87	109	2,206
1963	339	90	114	89
1964	957	94	118	475
1965	24,326	86	105	8,341

[1] Data for 1952–1964 are from Pennoyer and Stewart (1967) and from Alaska Department of Fish and Game (1968); remaining values are preliminary estimates furnished by the Alaska Department of Fish and Game.

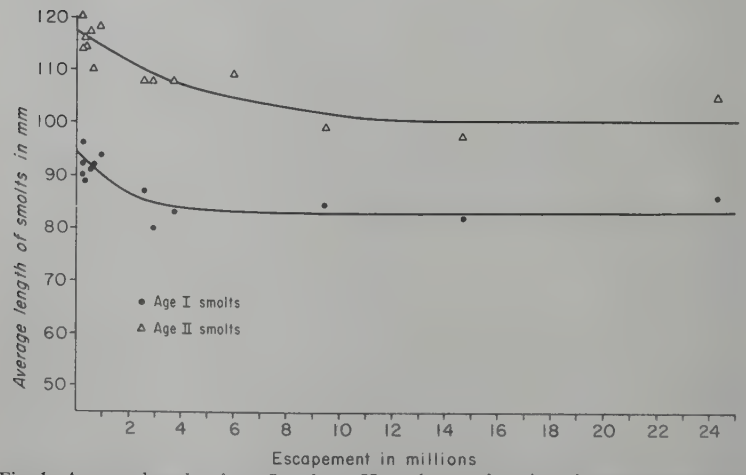

Fig. 1. Average lengths of age I and age II smolts as a function of parent escapement size in the Kvichak River, 1955–1968. Equation for the curve fitted to the age I smolt data is $y = 83.22 + 11.26 \cdot e^{-.63x}$, and that for the age II smolt data is $y = 101.02 + 16.22 \cdot e^{-.24x}$.

The observed relationships are expressed by negative exponential curves of the form $y = a + be^{-cx}$, fitted to the data by a non-linear regression technique (Gales 1964).

It may be assumed that the escapement of close to 25 million spawners in 1965 is perhaps the largest escapement to the Kvichak River since the inception of the commercial fishery. The data suggest that, for the observed escapement range, the young fish will not migrate to sea as age I smolts unless they have reached an average length of about 80–85 mm, and smolts of age II have reached an average length of about 100 mm or more. Since kokanee salmon have never been observed in Iliamna Lake and age III smolts constitute a negligible group, either the food supply is sufficient for all fish which do not migrate at age I to reach an average size of about 100 mm or the slower growing fish are more easily captured by predators.

The statement on average minimum size at time of migration as age I smolts can be verified by observations on the juvenile salmon in Iliamna Lake. Personnel of the Fisheries Research Institute have sampled the juvenile salmon in Iliamna Lake every year in August and September since 1962 (Kerns 1965, 1966, 1968). The maximum and average sample mean lengths of fingerlings calculated as of September 1 are given in Table 2. Also given is the computed daily increase in length, based on repeated sampling each year at the same locality from the latter half of the summer season; this growth rate is assumed to have been maintained from June to September. Such data may yield a higher growth rate during the first part of the summer than actually took place. In some years the maximum sample mean length of fingerlings, computed as of June 1, approached the length at which smolts migrate to sea as age I, but the computed average lengths were substantially smaller with one exception. In Iliamna Lake, the smolt out-migration is brief and essenti-

Table 2. Growth in length of yearling sockeye salmon in Iliamna Lake from June to September, 1962–1967.

Year	Sample mean length on Sept. 1, mm		Estimated average daily increase in length, mm	Calculated length on June 1, mm	
	Maximum	Average		Maximum	Average
1962	102.1	90.8	.18	85.9	74.6
1963	104.1	100.0	.20	86.1	82.0
1964	108.8	96.2	.37	75.5	62.9
1965	117.3	110.3	.58	65.1	58.1
1966	114.8	110.7	.56	64.4	60.3
1967	104.0	90.4	.27	79.7	66.1

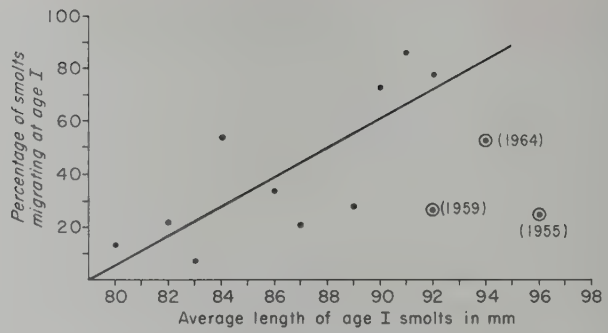

Fig. 2. Regression line of percentage of smolts migrating at age I on the average size of age I smolts, 1953–1965. Data for the years 1955, 1959, and 1964 are not included in the calculation of the regression line $y = -437.3 + 5.54x$.

ally over by the first week of June, unlike in some other lakes of Bristol Bay, where migration may extend through the month of June and part of July. In the Kvichak River system, therefore, it is possible to specify the time at which smolts must average a minimum size to migrate.

Finally, one could expect the proportion of age I smolts produced from an escapement to increase with an increase in average length of age I smolts. Data published by Pennoyer and Stewart (1967) on average smolt length and proportions of smolts of age I and age II produced from an escapement have been plotted in Fig. 2. At first glance a linear relationship seems to be nonexistent. However, when the three aberrant points representing the proportions of smolts from the spawnings in 1955, 1959, and 1964 migrating at age I are excluded, a reasonably well-defined relationship emerges. The larger the average length of age I smolts, the larger the proportion of the year class that migrated at this age.

An explanation for the three aberrant points must be sought elsewhere. All three represent production from a pre-peak year class of the Kvichak River sockeye salmon cycle. The low percentages of age I smolts produced from the spawning in 1955, 1959, and 1964 should be viewed perhaps as a result of the cyclic variability in run magnitude. The age II smolts spent their last year of freshwater residence together with the fry of the subsequent peak year, and they may have survived better than smolts in the other years of the cycle since the rate of primary production shows a tendency to increase in the year following a peak cycle year (Baxter 1968).

Furthermore, the proportion of fish migrating to sea as age I smolts may only increase linearly with length of the juvenile salmon over a

certain size range. In years with a low biomass of juvenile salmon and a high growth rate and average length, the proportion of age I smolts produced from an escapement may decrease in a parabolic manner. This presumably was the case for the three aberrant years prior to the peak cycle year. KROGIUS (1961) has presented similar data from Lake Kuril pointing to a prolonged freshwater residence in years with low biomass of juvenile salmon relative to the food supply and hence increased growth rate. The secondary production in Iliamna Lake has remained fairly stable since observation started in 1962. Such suggestions can only be verified by further studies, but the substantially identical relationship for the three pre-peak years for which data exist strongly suggests that such a mechanism must be operating.

LENGTH AT MATURITY OF THE KVICHAK SOCKEYE SALMON

Since 1957 the mean length of the returning mature sockeye salmon to the Kvichak River has varied from about 540 to 580 mm for three-ocean females and from about 480 to 520 mm for the two-ocean females. Although the males are larger, a similar range of size variation has been observed for the males (Table 3). Length is defined as the distance from the middle of the eye to the fork of the tail.

Population density has been expressed as the total size of the run in any one year by combining the catch and escapement of all age groups which returned to the Kvichak River in a year. A negative exponential

Table 3. Average lengths of Kvichak sockeye salmon in the escapements, 1957–1968 (mm).

Year	Total Kvichak/Naknek run in millions	Male		Female	
		2-ocean	3-ocean	2-ocean	3-ocean
1957	8.183	518.6	571.6	503.2	552.0
1958	1.830	537.2	591.1	516.8	567.7
1959	5.427	521.4	582.4	510.5	558.9
1960	26.547	488.1	567.5	471.4	535.0
1961	12.314	515.1	574.1	503.6	563.2
1962	5.676	524.0	578.3	511.3	562.3
1963	2.405	529.3	599.1	513.7	571.7
1964	4.799	501.7	577.4	487.1	567.2
1965	44.358	493.9	560.8	477.2	540.4
1966	10.364	521.8	577.4	503.8	556.0
1967	6.512	537.6	597.1	518.6	578.1
1968	4.963	510.9	591.1	493.3	574.8

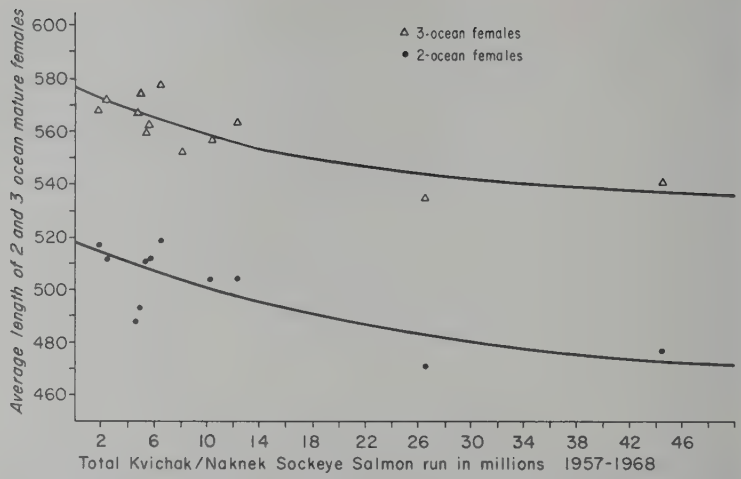

Fig. 3. Average length of returning female sockeye salmon as a function of total return, 1957–1967. Equation for two-ocean females is $y = 462.64 + 53.64 \cdot e^{-.037x}$ and that for three-ocean females is $y = 532.23 + 44.61 \cdot e^{-.53x}$.

relationship was found between the two variables for runs up to 26 million fish; but no further reduction in average length was observed, for example, in 1965 when 44 million fish returned (Fig. 3).

Changes in average length of a given age group of mature salmon have been described for other populations. KROGIUS (1960) describes regular periodic fluctuations in length of sockeye salmon from Lake Dalnee. BIRMAN (1964) brings out the interesting fact that not only is length of the salmon feeding in the sea inversely related to population density, but the total quantity of feeding salmon of all species affect the final size of a species, even in a year where this species may not be particularly abundant. He demonstrated that the size of the mature Bolsheret chum salmon was inversely related to the magnitude of the pink salmon runs in the same year. EGOROVA (1964) relates age at maturity of the Ozernaya sockeye inversely to the magnitude of the runs.

The authors cited above relate these manifestations to competition for food. However, it does not seem reasonable to postulate a general shortage of food in the ocean since the two ocean age groups of Kvichak sockeye salmon together number in any year at most between one and two hundred million individuals which migrate widely. Even if all species of salmon were considered together the magnitude is small compared with the abundance of other marine species. Still this does not preclude the existence of local shortage of food.

Table 4. Average index catches and weights of pelagic fish in Iliamna Lake, 1962–1967.

Year	Fry		Yearlings		Threespine sticklebacks		Relative total biomass
	Average catch per set	Average weight, in g	Average catch per set	Average weight, in g	Average catch per set	Average weight, in g	
1962	21.8	1.3	93.3	9.4	141.3	.8	1018
1963	27.8	2.1	12.0	9.0	24.3	.8	186
1964	.9	1.5	20.6	8.0	96.3	.9	253
1965	4.4	2.2	3.6	11.2	86.7	.9	128
1966	151.7	1.5	.9	13.1	40.4	.7	268
1967	67.6	2.1	80.9	6.6	38.3	.7	703
Average for all years		1.78		9.55		.8	

In the sea it is a difficult task to ascertain the abundance of food at one specific place and at a specified time. But, since growth of juvenile salmon in the Iliamna Lake nursery area and length at seaward migration seemingly follow the same pattern as growth of maturing salmon and their length at maturity in the sea, these problems can better be studied in a restricted freshwater ecosystem such as that of Iliamna Lake.

GROWTH OF JUVENILE SOCKEYE SALMON IN RELATION TO FOOD SUPPLY

Threespine sticklebacks, sockeye salmon fry and yearlings inhabit the limnetic zone of Iliamna Lake. Ninespine sticklebacks, smelts, and a few fish of other species are found also; but they make up a negligible part of the biomass of pelagic fish and can be ignored. The average weights of age I threespine sticklebacks and sockeye fry and yearlings in index catches in the years 1962–1967 are given in Table 4, based on data published by KERNS (1965, 1966, 1968). Whereas the average weight of age I sticklebacks has remained almost the same in the last 6 years, the weights of fry and yearlings have varied and have reflected changes in total biomass of limnetic fish. For all years, the average weight of fry was 1.78 and that of yearlings 9.55, or a ratio of 5 : 4. But within the lake

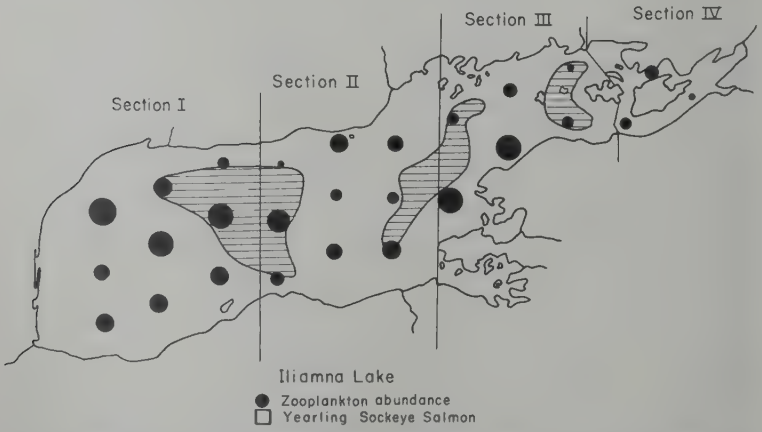

Fig. 4. Standing crop of zooplankters and maximum density of sockeye salmon yearlings in Iliamna Lake, August, 1967. Cross-hatched areas correspond to average catches of 300 yearlings or more per tow. Smallest circle indicates 3–4,000 and largest circle, 12–14,000 zooplankters per cubic meter. (Data on fish abundance given by KERNS (1968) and plankton abundance from unpublished data provided by Mr. T. GUNNERØD.)

there are great differences in length. For the sake of convenience the lake is divided into four main sections, numbered I to IV, from west to east (Fig. 4). It has been known for some time that the average length of yearlings in any one year in the western part of the lake (section I) is greater by about 20 per cent than that of fingerlings in the eastern part (section IV) (Kerns *et al.* 1963). These differences can be related to the standing crop of zooplankton which has been estimated from samples taken with a No. 6 mesh, ½-m open net from bottom or 100 m to surface. Although such a sampling does not yield any absolute estimate of the rate of production, the standing crop of zooplankters toward the end of August, when sampling of juvenile sockeye salmon normally takes place, serves as a relative measure of the food potential at this time of the year.

The average number of zooplankters per cubic metre in sections I to IV for the years 1963–1968 were 10,050, 8,938, 7,196, and 6,201 respectively. This seemingly direct relationship to average length of yearling sockeye salmon which decreased from section I to section IV for the same years disappears when the average length of yearlings within a section is plotted against the standing crop of zooplankters there in any one year (Fig. 5). If a regression line is fitted between observed average length and corresponding zooplankton abundance, the hypothesis that the slope

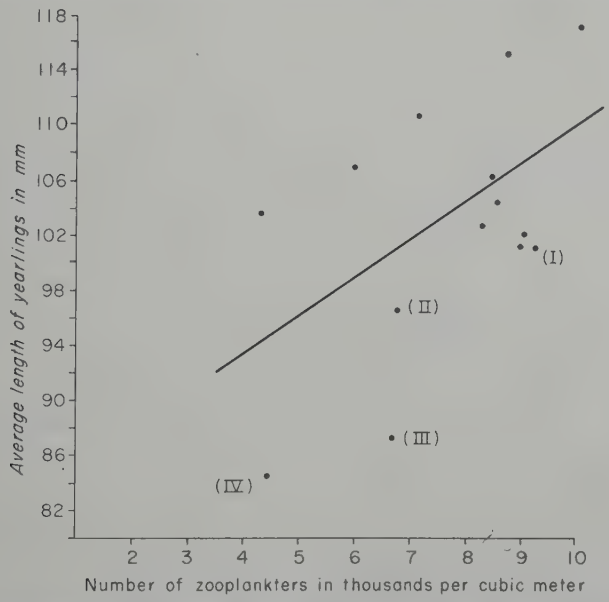

Fig. 5. Regression line of average lengths of yearling sockeye salmon and standing crop of zooplankters by lake sections (sections indicated in parentheses for 1967).

of this line is zero is barely rejected at the 95 per cent confidence level. ($t = 2.33$, 15 d.f.) and the hypothesis is accepted at the 99 per cent level.

Two factors add to this variability. First, the larger average lengths of yearlings in the two lower sections I and II may be due to an immigration of the fastest growing fish from the two upper sections III and IV and length may not be directly related to observed plankton abundance. A majority of fish spawn in sections III and IV and the resulting progeny move down Iliamna Lake to the outlet in the western end of section I during their freshwater residence.

Secondly, the distribution of yearlings in 1967 (Fig. 4) in relation to observed plankton abundance registered at the different stations in that year include heavy abundance of yearlings at places both with high and low abundance of zooplankton. This raises doubt as to the suitability of an average zooplankton abundance for a section as an index of food potential unless the juvenile salmon constantly and rapidly move around feeding. It is difficult to pass judgment on this question from the existing tow net data which give fish abundance only once during each season. A rapid dispersal of the juvenile salmon is not apparent. Since 1962 a centre of heavy yearling concentration in the lower part of Iliamna Lake has been associated with a large biomass of juvenile salmon and ensuing population pressure which forces a more widespread dispersal.

Too many factors are therefore confounded at the present time to state clearly the dependence of growth of juvenile salmon upon the availability of food except in a rather approximate manner.

There are indications that other growth inhibiting factors related to population density are operating. Two points deserve mention. In 1967, a year with the largest biomass of juvenile salmon present for those years where corresponding plankton data are available, the average length of the yearlings in all sections were substantially lower (sections I, II, and III) or equal (section IV) to the smallest average length observed in other years at a corresponding plankton density. Secondly, there is an asymptotic lower limit for average length of migrating smolts, both of age I and age II smolts. Both facts lead one to hypothesize that the depression of growth rate in years with a high biomass of juvenile salmon is due to space factors. The same may be true for the immature fish feeding in the sea. These results are in accord with those presented by Johnson (1965) from Babine Lake. As to the nature of such growth inhibiting factors related to population density Johnson summarized pertinent studies. But to date the proposed factors are merely indicative of those operating in sockeye populations and worthy of further investigations. It should be illustrative to study not only the total number of zooplankters but also their availability to sockeye salmon under different fish densities.

As a consequence, the capacity of the nursery area in Iliamna Lake can be measured adequately by the number of smolts produced from an escapement, especially since the survival rate of smolts to mature salmon is not closely tied to average length of the smolts.

SMOLT PRODUCTION IN THE KVICHAK SYSTEM IN RELATION TO MAGNITUDE OF PARENT ESCAPEMENT

Basically, two groups of points are available for placing an upper limit on the nursery capacity. One group includes the numbers of smolts produced from a series of small escapements, and another group the numbers of smolts produced from three peak years. In Fig. 6 are plotted the numbers of smolts produced and the magnitudes of the corresponding parent escapements for all years. The smolt production from the 1960 escapement may have been underestimated because heavy iceflow prevented sampling for extended periods when age II smolts migrated to sea in spring of 1963. Another estimate can be made by assuming that the ratio between index catches of smolts by fyke net in 1963 and 1968 should approximate the ratio of the average number of fingerlings caught by tow net in Iliamna Lake in the previous fall. In 1962, an average of 93.3 fingerlings was caught per haul, whereas an average of 80.9 yearlings was taken per haul in 1967. Thus, the expected index catch for age II smolts in 1963 would have been 7.7 million instead of the observed index catch of 5.2 million; the true value may lie somewhere between.

Two logistic curves of the form $y = a/(1 + e^{-(b + cx)})$ were fitted to the data, and the two values for the smolt index for 1963 were used. Smolt production increased as magnitude of parent escapement increased until an asymptotic limit was reached. In both cases it appears that the asymptotic limit for the number of smolts that can be produced from one

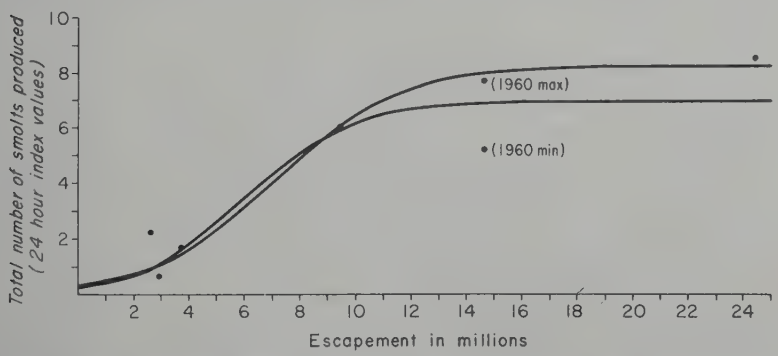

Fig. 6. Total numbers of smolts produced from escapements in the Kvichak system, 1953–1965. Equations for the two logistic curves are $y = 8.14/(1 + e^{3.20-.46x})$ and $y = 6.83/(1 + e^{3.19-.55x})$.

escapement in Iliamna Lake is close to the 1965 production value, although substantially smaller escapements will yield about the same number of smolts. Some confirmation may be derived from historical data for the Kvichak stock. In order to arrive at an escapement of 25 million spawners, it is necessary to postulate unrealistic low fishing mortalities except for the period 1936–1938. In 1936 the Kvichak catch numbered 16.8 million fish, in the following year 14.0 million, and in 1938 21.0 million; and the escapements must have been at least the same size (Mathisen 1965). In other years the commercial catches never reached such magnitudes and it is not reasonable to suspect the escapement to have reached the 1965 value.

It is an important fact that during the period 1936–1938 the pattern of the Kvichak cycle changed from a peak run and one or two very strong subdominant runs to one exceedingly strong peak run and small runs. The latter pattern has persisted to the present. Were several strong year classes to be produced again in succession, there would be a sustained cropping rate of zooplankters and the total standing crop may decline drastically relative to the present-day situation. Zooplankton production may then exert a more direct effect on growth and survival of the juvenile sockeye salmon than observed today.

SUMMARY

1. Catch and escapement of Kvichak River sockeye salmon (*Oncorhynchus nerka*) and smolt production from Iliamna Lake, the nursery area, have been determined annually since 1955. Since 1962, information has been collected on growth and abundance of fry and yearlings and zooplankton production in Iliamna Lake.
2. Growth in length of smolts can be expressed as a negative exponential function of population density. A similar relationship exists for maturing salmon on their return from the ocean to the Kvichak River.
3. There is no strong correlation between the growth of juvenile salmon in Iliamna Lake nursery area and the standing crop of zooplankters. Other effects of crowding on growth need to be investigated.
4. An asymptotic limit for the number of smolts produced in the nursery area has been computed, but it may be valid only for a single-peak cycle, the current pattern of run variability in the Kvichak River.

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THE HALIBUT GILLNET FISHERY IN WEST FINNMARK

Analysis of Landings Data from Øksfjord 1955–65

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INTRODUCTION

In 1936 gillnet fishing for halibut was started in Norway (Devold 1938). One of the main localities for this autumn–early winter fishery is the deep parts of Altafjord in West Finnmark with its tributaries and entrances.

Detailed studies of the fishery and the stock of halibut in this area were carried out during the years 1956 to 1960 (Olsen 1956, Tjemsland 1960, Olsen and Tjemsland 1963, Mathisen and Olsen 1968). The findings of these investigations provided the main basis for revisions of existing regulations being in force for this fishery since 1937. The first revision was introduced in 1956 when the fishing time was increased to the end of December from, previously, December 15; and the second one in 1962, from which year the closed season started on January 21.

Estimates of mortality and the likely effects of the fishery on the stock were reported by Mathisen and Olsen (1968). The present data throws some further light on the dynamics of this stock of large mature halibut, which for most practical purposes can be considered as exploited by the gillnet fishery only during the short period of the year when these large fish penetrate into the deep fjords of Northern Norway to spawn.

MATERIAL AND METHODS

The Official Statistics of Norway give catch of halibut by months, but no published commercial statistics exist for the gillnet fishery alone or for the effort extended in this fishery.

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Contribution given in honour of Gunnar Rollefsen at his 70th birthday.

Table 1. Records of gillnet caught halibut landed in Øksfjord during the seasons 1955 to 1964–65.

Year	Month	Landings in kg	No. of men per vessel	No. of landings	No. of men times no. of landings	CPUE
1955	Oct.	1.580	3.5[1]	90[1]	315	5.0
	Nov.	5.782	3.8[1]	100[1]	380	15.2
	Dec.[2]	7.768	4.1[1]	60[1]	410	18.8
	Nov.–Dec.	13.550	—	160[1]	790	17.2
1956	Nov.	8.232	3.8[1]	140[1]	532	15.5
	Dec.	20.286	4.1[1]	143	586	34.6
	Nov.–Dec.	28.518	—	283[1]	1118	25.5
1957	Oct.	2.146	3.5[1]	47	165	13.0
	Nov.	5.100	3.8[1]	54	205	24.9
	Dec.	19.489	4.1[1]	96	394	47.9
	Nov.–Dec.	24.589	—	150	599	41.1
1958	Oct.	2.369	3.5[1]	35	123	19.3
	Nov.	3.039	3.8[1]	38	144	21.1
	Dec.	13.523	4.1[1]	53	217	62.3
	Nov.–Dec.	16.562	—	91	361	45.9
1959	Oct.	2.270	3.5[1]	27	95	23.9
	Nov.	2.817	3.8[1]	32	122	23.1
	Dec.	8.443	4.1[1]	44	180	46.9
	Nov.–Dec.	11.260	—	76	302	37.3
1960	Oct.	1.576	3.5[1]	37	130	12.1
	Nov.	4.172	3.8[1]	35	133	31.4
	Dec.	5.691	4.1[1]	42	172	33.1
	Nov.–Dec.	9.863	—	77	305	32.3
1961	Oct.	1.946	3.5[1]	40	140	13.9
	Nov.	5.256	3.8[1]	44	167	31.8
	Dec.	9.842	4.1[1]	47	193	51.0
	Nov.–Dec.	15.098	—	91	360	41.9
1962	Nov.	3.128	3.8	18	68	46.0
	Dec.	12.969	4.1	46	187	69.3
1963	Jan.	9.310	4.6	31	143	65.1
1962	Nov.–Dec.	16.097	—	64	255	63.1
1963	Oct.	1.162	2.3	9	21	55.3
	Nov.	2.535	3.1	12	37	68.5
	Dec.	14.745	3.8	43	163	90.4
1964	Jan.	3.170	4.4	8	35	90.6
1963	Nov.–Dec.	17.280	—	65	200	86.4
1964	Oct.	2.064	2.9	13	37	55.7
	Nov.	5.039	3.0	20	59	85.4
	Dec.	7.748	3.5	36	126	61.5
1965	Jan.	489	2.8	5	14	34.9
1964	Nov.–Dec.	12.787	—	57	185	68.0

[1] Estimated figures. [2] Closed season starting 15 December.

Table 2. Monthly weight distributions for gillnet caught halibut landed at Øksfjord.

W kg	1961–62					1962–63					1963–64					1964–65				
	O	N	D	J	Σ	O	N	D	J	Σ	O	N	D	J	Σ	O	N	D	J	Σ
5–9	2	4	2	35	43	—	1	14	16	31	35	64	34	10	143	—	2	29	44	75
10–14	3	11	13	72	99	4	3	28	49	84	30	37	61	26	154	2	7	42	72	123
15–19	9	8	14	90	121	2	6	20	36	64	20	17	59	17	113	2	8	31	62	103
20–24	5	13	11	54	83	2	7	33	17	59	19	10	61	21	111	5	14	28	46	93
25–29	11	23	28	44	106	3	11	60	29	103	12	20	70	20	122	11	43	67	43	164
30–34	11	23	28	29	91	1	19	59	22	108	18	22	97	16	153	17	56	83	22	178
35–39	10	22	27	23	82	5	26	56	13	100	7	20	54	13	94	10	25	43	21	99
40–44	2	19	16	13	50	4	11	19	11	45	4	10	29	8	51	10	18	32	20	80
45–49	5	5	10	18	38	—	1	11	6	18	1	1	14	5	21	6	8	13	8	35
50–54	—	2	5	15	22	2	—	11	3	16	3	1	14	3	21	1	1	8	7	17
55–59	—	4	1	10	15	—	3	2	3	8	—	—	5	5	10	1	2	5	2	10
60–64	1	—	2	8	11	1	—	—	3	4	1	—	6	—	7	—	1	5	7	13
65–69		3	—	10	13	—	—	—	4	4	—	—	2	1	3	—		2	5	7
70–74		1	1	8	10	—	—	—	1	1	—	—	6	1	7	—		2	2	4
75–79		1	—	6	7	—	1	3	2	6	1	—	2	—	3	—		—	3	3
80–84		—	1	5	6	1	—	2	3	6		—	1	1	2	—		2	3	5
85–89		1	—	7	8		1	1	2	4		2	—	2	4	—		2	3	5
90–94		1	1	2	4		—	1	—	1		—	2	1	3	—		2	4	6
95–99							1	1	2	4		—	2	3	5	2		1	3	6
100–104								1		1		—	—	3	3			3	1	4
105–109												—	3	2	5			3	4	7
110–114												—	1	2	3			1	3	4
≧115												1	1	5	7			7	4	11
Total	59	141	160	448	808	25	90	322	222	659	151	205	524	165	1045	67	185	411	389	1059
$\overline{W}$	29.5	33.5	32.6	29.3	30.7	33.5	34.1	29.4	27.6	30.5	21.0	20.7	29.8	35.9	27.7	36.1	31.5	33.3	29.5	31.2

Through the courtesy of Njord Handels og Industri A/S, the only fish packing and processing company in Øksfjord, where a fair proportion of all gillnet caught halibut in West Finnmark is landed, a series of detailed landing statistics for this fishery was compiled for the period 1955–1965 (Table 1). Some data on relative effort were also collected and the material thus comprises monthly (since 1961 also weekly) records of all landings of gillnet caught halibut; the number of landings made, and since 1962 also the number of men, and some information on the amount of gear in relation to vessel size and number of men. For the four last seasons data are available on the size distribution of the landings in terms of weight (Table 2).

Records are available of the number of landings from 1957 onwards and for the last three seasons also of the number of men for each vessel and landing. These data show quite clearly that the average number of men per vessel increases from October to December–January, probably because the larger vessels do not start halibut fishing until the latter part of the season when catches are best.

For the season of 1962–63 there are also data on the amount of gear used, and these reveal a nearly linear relationship (Table 3) between number of nets and number of men per vessel. Thus the effective effort is directly proportional to the number of men per vessel, and the landing data have to be corrected for the seasonal change in vessel size, or average number of men per vessel, to facilitate unbiased estimates of catch per unit of effort (CPUE). In recent years there has been a continuous trend of reducing the number of men required to operate these fishing vessels, and the monthly estimates of average number of men per vessel for 1962 were therefore used as weighting factors for all previous years.

Table 3. No. of men and average no. of nets used for 11 vessels in the 1962–63 season.

No. of men	Average no. of nets
2	23.3
3	24.5
3	26.4
4	31.5
4	31.8
4	38.6
4	45.0
5	36.0
6	72.0
6	77.0
7	88.3

The estimates for November and December of CPUE were applied to the official statistics of total catch of halibut in Finnmark during the last quarter of each year to calculate the total effort required to catch an equivalent quantity of halibut if fishing with gillnets only (Table 4). Since halibut landings in October are always relatively small the bias introduced by using the combined CPUE estimates for November–December only is probably not very significant.

SIZE DISTRIBUTION

Table 2 gives the monthly weight distribution in 5 kg groups of all gillnet caught halibut landed in Øksfjord during the fishing seasons 1961–62 through 1964–65. Frequency distributions for the total material, October–November–December combined and for January respectively are plotted for each year on Fig. 1. The bimodal type of distribution is probably caused by the great sex difference in growth rate.

In all seasons except 1963–64 the halibut caught during October–December were generally larger than those taken in January. This is in keeping with previous findings from the detailed investigations of 1956 to 1960 (Olsen 1956, Tjemsland 1960) that the older fish which have spawned earlier generally arrive on the spawning grounds before the first time spawners; which for halibut in the Altafjord area usually do not appear before some time in January.

However, in the 1963–64 season the spawning run apparently occurred earlier than normal and many relatively small-sized halibut were caught before Christmas. When January came catches were declining and most of the season was presumably over by then.

The figure shows no general trend of decreasing fish size over the years. If anything, there was a slight increase in the relative numbers of medium sized fish and the proportion of large halibut, over 50 kg say, remained fairly constant. This size distribution is very similar to that established for the period 1956 to 1960, and although it is known that a gradual increase from 16″ to 18″ mesh size of the halibut nets did take place in recent years, it is nevertheless safely concluded that no dramatic change in size composition has occurred from the first to the second five-year period.

CATCH AND EFFORT

On the top of Fig. 2 are plotted the landings in Øksfjord during October–November–December, of all gillnet caught halibut and the corresponding total landings of halibut in the county of Finnmark. These also include a quantity taken with longlines and trawl (mainly immature fish).

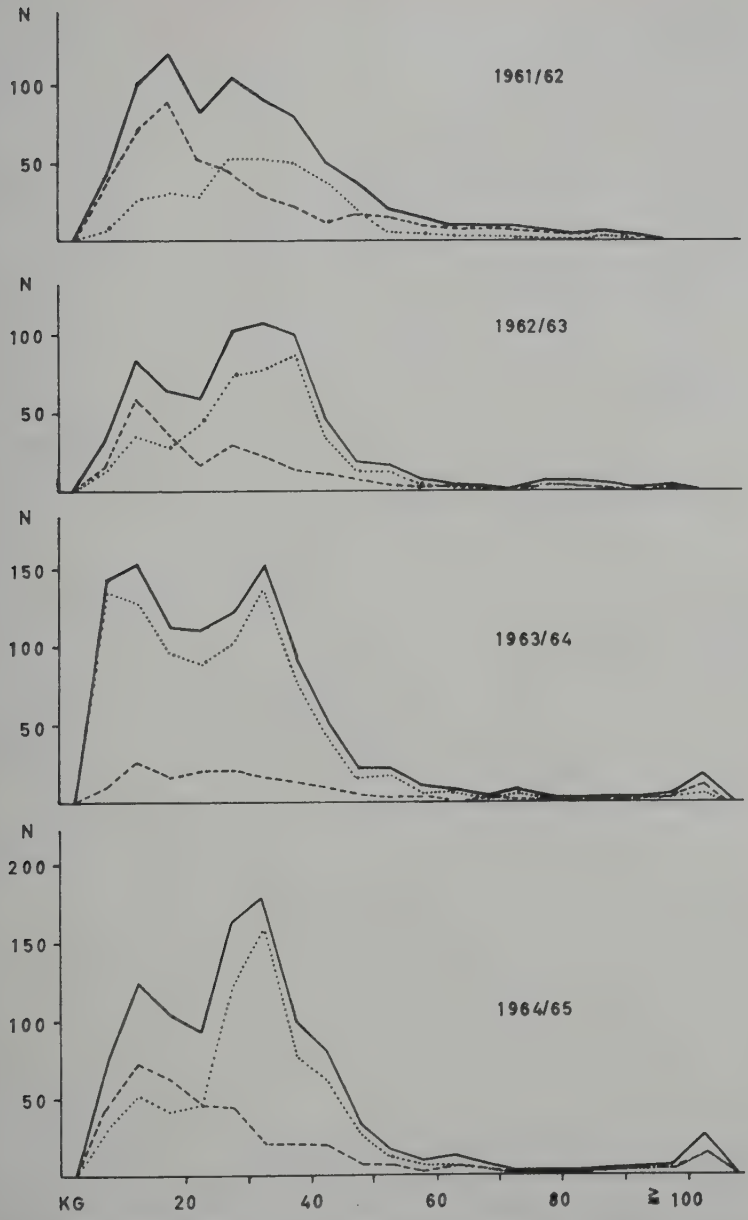

Fig. 1. Size distributions of gillnet caught halibut landed at Øksfjord. Solid line: total. Dotted line: October/November/December. Broken line: January.

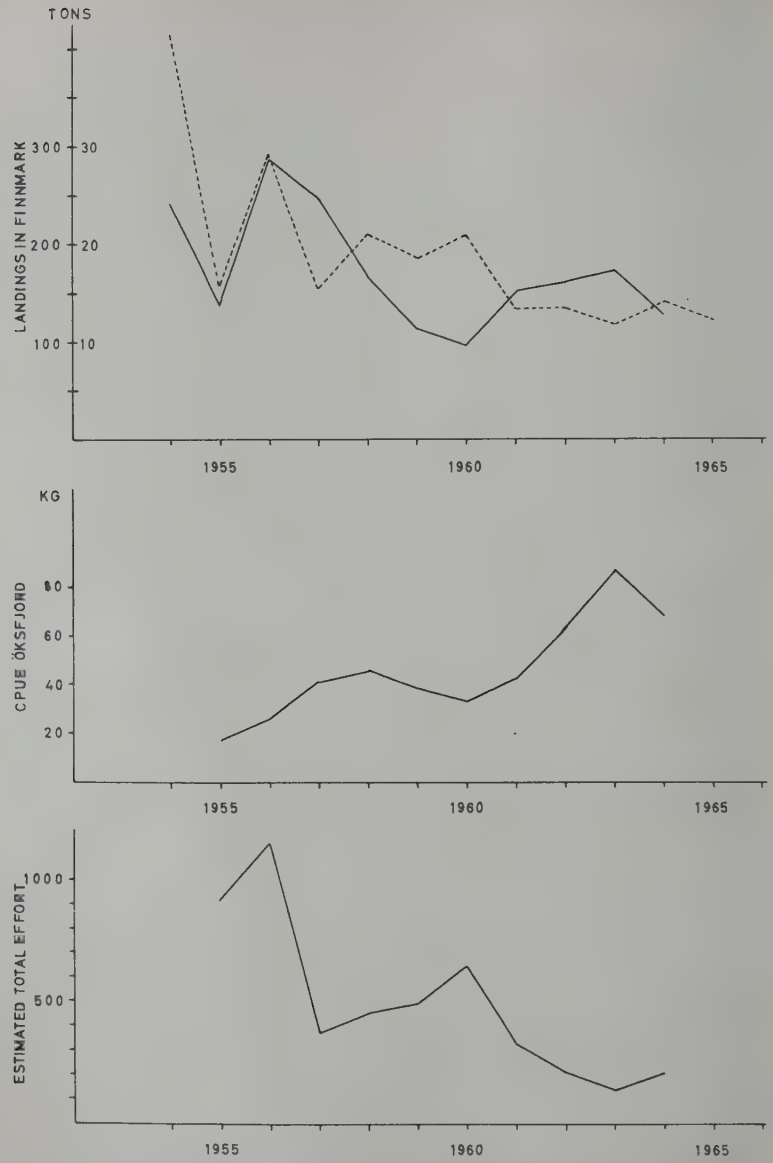

Fig. 2. Top, solid line: gill net caught halibut landed at Øksfjord in November/December. Broken line: total halibut landings in Finnmark during October/November/December. Middle: catch per unit of effort (CPUE) estimated from statistics of landings at Øksfjord in November/December. Bottom: estimated total effort of the halibut fishery in Finnmark during last quarter of the year.

The figure confirms that Øksfjord is a main landing place for the halibut gillnet fishery in the area and accounts for about 10 per cent of all halibut landed in Finnmark. Thus, there is good reason to assume that any trend in the halibut stock of the area would be manifest in the fishery out of this port.

The landing statistics for 1955 to 1965 shows a general trend of decreasing halibut landings in the last quarter of the year both for the whole county and for the gillnet fishery out of Øksfjord.

This decrease has taken place at the same time as a marked increase in CPUE has been experienced (Fig. 2, middle) and, consequently, the estimated total effort of the fishery has decreased to about one-fifth of the level in the mid-1950's (Fig. 2, bottom, Table 4).

The rise in CPUE has been most spectacular and continuous for the month of November, but also for December and October a great increase was apparent (Table 1), and on an average for November and December combined, CPUE more than tripled during the ten-year period studied.

DISCUSSION

There may be several reasons for the spectacular rise in CPUE during the period covered by this study. For December there was at first a great increase in the years 1956, 1957 and 1958. This was most probably a direct result of the new regulations extending the season to the end of December and the changeover from hemp to nylon nets, which took place gradually during these years. This gear innovation was followed by a gradual increase in mesh size from the usual 16″ nets to 18″, and even

Table 4. Total catch of halibut landed in Finnmark during October/November/December and estimated total effort for the same period.

Year	CPUE Nov./Dec.	Catch in Finnmark Oct./Nov./Dec.	Estimated total effort
1955	17.2	157	913
1956	25.5	292	1145
1957	41.1	153	372
1958	45.9	210	457
1959	37.3	184	493
1960	32.3	209	647
1961	41.9	136	324
1962	63.1	134	211
1963	86.4	119	137
1964	68.0	142	209

Table 5. Records of catch and effort in 1962/63 for 12 vessels using nets of different mesh sizes.

Week No.	16″ and 18″ mesh			18″ and 20″ mesh			All nets		
	Catch kg	No. of nets	kg/net	Catch kg	No. of nets	kg/net	Catch kg	No. of nets	kg/net
46	320	186	1.7	644	215	3.0	964	401	2.4
47	469	204	2.3	31	30	1.0	500	234	2.1
48	421	165	2.6	409	220	1.9	830	385	2.2
49	1719	556	3.1	1944	400	4.9	3663	956	3.8
50	1264	392	3.2	549	205	2.7	1813	597	3.1
51	1714	485	3.5	1595	320	5.0	3309	805	4.1
52	169	70	2.4	—	—	—	169	70	2.4
1	199	60	3.3	179	30	6.0	378	90	4.2
2	1761	248	7.1	2887	355	8.1	4648	603	7.7
3	2451	332	7.4	1118	105	10.6	3569	437	8.2
4	337	55	6.1	3101	270	11.5	3438	325	10.6
45–48 (Nov.)	1469	627	2.3	1084	465	2.3	2549	1092	2.3
49–52 (Dec.)	4866	1503	3.2	4088	925	4.4	8954	2428	3.7
1–4 (Jan.)	4748	695	7.0	7285	750	9.7	12033	1445	8.3
Total	11183	2825	4.0	12457	2130	5.8	23540	4955	4.8

20″ used by some vessels, while the dimensions of the nets themselves remained unchanged. It is interesting to note that the shift to larger mesh sizes was already started voluntarily before the 18″ mesh was prescribed by the new regulation in 1961 as a direct result of the successful experiments with large meshed nets carried out by the Institute of Marine Research from 1957 to 1960.

This mesh increase was probably partly responsible for the more than doubling of CPUE which occurred after 1961 and which was apparent throughout the season. Some data from 1962–63 (Table 5) of catch rates for 16″ and 18″ nets compared with 18″ and 20″ nets suggest that the immediate effect of the mesh size increase would be of the order of 40% to 50%. Any long term effects of increasing the exploitation age, as discussed by Mathisen and Olsen (1968) would not take effect immediately, and hence, the rising CPUE must also have been caused by other factors than the use of larger meshed nets.

There is no evidence suggesting that the rise in CPUE estimates could be related to increased effective fishing time of the nets in recent years; in fact, any trend here would be towards decreasing fishing time when nylon nets were introduced because the fish die quickly in such nets and the quality then deteriorates.

One possible cause is the increase in the minimum landing size of halibut from 50 cm to 65 cm introduced in 1956. This regulation certainly reduced the fishery for small, immature halibut at the Finnmark coast, and any effects of the reduced fishing mortality of these age groups (3–5 years) would not be felt in the gillnet fishery for mature halibut until at least 6–7 years later.

Finally, one should consider the apparent fall in total effort of the Finnmark halibut fishery, which in itself is probably related to a gradual change during the same period in the structure of the fishing fleet and the overall reduction in the number of fishermen. In Fig. 3 CPUE is plotted against the two years sum of estimated total effort. This indicates a direct relationship between CPUE and effort which for the range in total effort experienced during the 1955–65 period could well account for the observed increase in CPUE.

This relationship might be composed of two components. Firstly, it could reflect a true density change resulting from variations in fishing mortality. However, it is also likely that the reduced and low participation in this fishery in recent years, which is conducted in fairly restricted localities, has had a direct and immediate effect on the efficiency of the operations for the individual vessels, allowing more careful selection of the fishing places for the nets and practically eliminating any chance of entangling or conflict between different vessels.

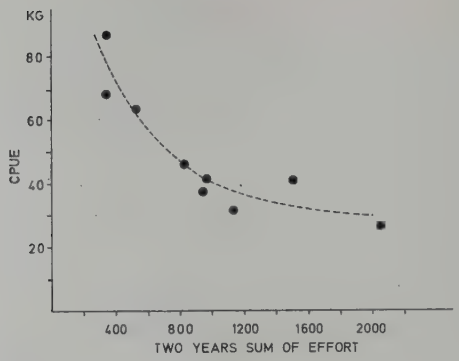

Fig. 3. Estimates of catch per unit effort (CPUE) at Øksfjord for November/December plotted against two year sums of estimated total effort for the county of Finnmark during October/November/December.

The present data have thus demonstrated that the trend of decrease in the halibut landings in Finnmark from 1955 onwards was most likely caused by reduced fishing effort, while in the gillnet fishery for mature halibut the CPUE increased greatly. This increase was partly caused by more efficient nets and less competition on the fishing grounds, but it also reflects a real increase in fish density resulting from the lower fishing mortality in the mature stock, the increased exploitation age, and possibly improved recruitment to the mature stock resulting from the raising of the minimum landing size introduced in 1956.

SUMMARY

1. This study was based on statistics of gill net caught halibut landed at Øksfjord, West Finnmark from 1955 to 1965. For the most recent years some data on relative effort and weight distribution of the catches were also available.
2. Small annual fluctuations in size distribution of the catches occurred, but no consistent trend over the years were apparent.
3. During the 10 year period studied, halibut landings in the last quarter of the year decreased markedly both in the county of Finnmark as a whole and at Øksfjord. However, during the same period catch per unit of effort in the gill net fishery increased greatly, and consequently, the estimated total effort was very much reduced.

4. It is concluded that the reduced landings resulted mainly from reduced fishing effort while the increase in catch per unit of effort was partly caused by improved fishing nets and less competition on the fishing grounds, but was also reflecting a real increase in fish density.

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ON THE PROBLEM OF THE EFFECT OF FISHERIES ON FISH STOCKS

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When we consider the problem how the fisheries affect the fish stocks and their reproduction the most important and principal question arises whether the fish have ever encountered the influence of any factor similar to that of the fisheries. In other words, we ask if the fish have been able to adapt themselves to some influence which can help them to stand the fishing effect, or whether the fisheries are quite a new factor to them, and they are not prepared at all.

In ichthyological literature the effect of fisheries is, to some extent, considered similar to that of predators on the fish stock. The suggestion seems to be true for small sized abundant species which are, in fact, subject to such an influence under natural conditions. However, the fishing and predatory effects differ substantially. The fishery is usually based on the adult portion of the population, and due to longer contacts between the fishery and older age groups the numerical strength of the latter is drastically reduced. The "rejuvenation" process is always a consequence of the fishery. Predators, on the contrary, take younger age groups. The predatory effect never leads to rejuvenation of the population. Thus, the fishing effect is of specific character, and the majority of fish in their development and during the adaptation process to the environment have never encountered influences resembling the fishing effect under natural conditions. Furthermore, many biologically adapted features which are acquired due to evolution and advantageous to the fish under natural conditions are turning into disadvantageous habits, thus increasing the effect of fisheries on the stocks and the reproduction.

This can be illustrated by a number of examples (Table 1). In many fish species the bodies are covered with bone knobs, hooks and thorns,

Contribution given in honour of Gunnar Rollefsen at his 70th birthday.

Table 1. Adapted features in fish, their biological significance and negative role under condition of intensive fishing

Adapted features	Biological significance	Negative role under fishing conditions
1. Knobs, hooks and thorns on fish bodies, thorny rays in fins	Protection of fish, especially young from predators	Tangling in nets and difficulty in escaping through meshes
2. Height and width of fish bodies	Lower predatory effect on young fishes	Enmeshing in nets with relatively large meshes
3. Shoaling	Lower predatory effect	Efficient detection of shoals by echosounders and asdics
4. Multiage composition of a population	Increase in the reproductive ability of the population	Decline in the reproductive ability as a result of rejuvenation of the stock caused by intensive fishing
5. Gradually maturation of eggs and spawning in batches	Increase in the reproductive ability of a species	Due to longer stay spawners are more easily caught on spawning grounds
6. Low metabolism in winter during the period of maturation	Savings in energy	Higher accessibility to the fisheries
7. Ability of burying themselves in the ground	Protection from predators	Failure in escaping fish nets
8. Well developed receptive system in tuna	Detection of prey	Increase in the space between hooks and extension of longlines
9. High speed of movement in tuna	Chasing for prey, escape from predators	Spread of the area fished by a longline
10. Habit of avoiding zones with high velocities of water in the river in many anadromous fishes	Savings in energy during anadromous migrations	Better access to the fisheries in shallow localities in the river

and the fins have thorny bone rays. These peculiarities can be looked upon as an adapted protection of the species, especially the young, against predators. Due to these features the bycatch of young increases under intensive fishing since it is difficult for them to escape through the meshes of nets and trawls and easy to get tangled in the meshes of the different gears. The best evidence of the negative role of the morphological peculiarities is tangling of the young of sturgeon in fixed and drift nets. This greatly affects the fish stock.

Great width and height of a fish body protect the fish from predators.

In the fishery, due to the height of the body, young specimens are entangled in nets with rather big meshes. Flounder, bream and some other species may exemplify this fact. The peculiarities of their body form impede selective fishing.

Shoaling can, to a certain extent, be considered a means to protect the fish from predators. However, the fishery with modern scouting techniques is facilitated by the shoaling and yields good catches.

A multiage composition of a spawning population leads to some increase in the reproductive ability of a species. Intensive fishing may result in a rejuvenation of the stock by reduction in the older age groups in the spawning population and finally, lowering of the reproductive ability of the species.

The fecundity of fish increases when the eggs mature gradually and is spawned in batches. This enables the fish to use much more of the energetic resources of the body as compared to the case where all the eggs ripen at the same time. Under fishing conditions a gradual maturation makes females stay on the spawning grounds much longer, chances for catch, thus, increases.

A lower rate of metabolism in winter, in the period of gonad maturation is observed in many species of fish. The phenomenon enables a species to save some energy for spawning. Low mobility of fish in this period makes them more vulnerable to fishing gear. The winter fishery for carp is based on this peculiarity as the fish are taken in deeper hollows.

Many species of flat fishes bury themselves in the ground to escape predators. The same reaction in fish to a coming trawl is observed, but all their efforts are in vain when the trawl is too near.

Tuna possess a well developed receptive system which enables them to locate prey over a radius of several dozen meters. Owing to this peculiarity hooks can be arranged with wider spaces, say 70–100 m apart, and the longline stretched to over 100 km.

The great swimming speed of the tuna causes an expansion of the efficient area of a longline, and the efficiency increases in proportion to the speed of the tuna moving over the area. As a result, a harmless gear, as it may seem at first sight, turns into one of the efficient means in the marine fisheries. Let us assume that the average speed of tuna is as low as 5 km per day when the longline is arranged in the water; a longliner then can cover the area of 500 square km. Even if not more than 20% of the fish inhabiting the area are caught, the catch per day per longliner will correspond to a yield from an area of 100 square km. Actually, the tuna is moving much faster.

The sturgeons moving upstream to their spawning areas, avoid zones with high velocities of water. To save their energy they migrate over

shallow places where they are more easily caught by seines than in deeper places of the river.

It is very likely that far more examples can be given as evidence for how adapted features, biologically advantageous, may turn into disadvantageous habits under the condition of intensive fishing.

All these facts reveal that the effect of fisheries on fish stocks is related not only to the technical progress and its excessive scale, but also with the aspect that some adapted features in fish is counteractive under conditions of intensive fishing, thus making the effect of fisheries more pronounced.

Programmes of further investigations should include examination of adapted features in fish which tend to have counteractive effect under fishing conditions, as well as comparative studies of these features under natural and fishing conditions.

SUMMARY

It is demonstrated by examples that morphological, physiological and behavioural features of fish developed evolutionary and normally of protective value are directly disadvantageous to the fish when subjected to intensive fishing.

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EFFECTS OF OCEAN THERMAL STUCTURE ON FISH FINDING WITH SONAR

By

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THE ACTIVE SONAR FORMULA

The sonar equipment has become in common use in most modern offshore fisheries in the North Atlantic. The performance of the sonar in fish finding depends on a multitude of factors, such as the technical properties of the sonar itself (e.g. the frequency used), the self noise of the vessel, the skill of the operator and, not least, the environment in which the sound propagates. This paper deals with the effects of the ocean thermal structure on the sound propagation.

The noise limited active sonar equation can be presented in a general form:

$$M_n = (S_o + T - 2H) - (N + \Delta R)$$

where M_n is the signal to noise ratio (or the recognition differential), S_o is the original signal strength, T is the target strength (or its scattering cross section) and 2H is the two-way propagation loss in the water. N and ΔR present the self noise and the directivity index (i.e. the gain of the signal due to receiving directivity) respectively. In reverberation limited condition, the last term $(N + \Delta R)$ represents the reverberation level.

The noise level N depends on environmental noises, such as those caused by breaking waves, by noise making marine animals, rain, traffic, and first of all, by the ships' own noises carrying the sonar.

EFFECTS OF OCEAN ENVIRONMENT ON THE PROPAGATION OF SOUND

The sound impulse emitted by a sonar or an echo sounder is subject to a number of losses during its travel through the water: the absorption

Contribution given in honour of Gunnar Rollefsen at his 70th birthday.

loss in water, the geometrical spreading loss, surface scattering (reverberation), volume scattering and bottom reflection or scattering loss.

The absorption loss in water is greatly dependent on the frequency used by the sonar, and also depends on the temperature of the water:

$$a = \frac{0.17}{T + 18} f^2$$

where a is absorption loss, T is temperature of the water and f is the frequency. The surface scattering depends on the roughness of the surface (e.g. the wave height) and sonar frequency. The bottom scattering is a relatively complex function of the type of sediment, bottom roughness and frequency. The volume scattering depends on frequency and on the amount of scatterers (such as air bubbles, plankton and fish).

The geometrical spreading loss depends on the vertical distribution of the sound speed in the water. This aspect of the sound propagation is described in this paper in relatively easily measured and/or predicted ocean thermal structure parameters—sea surface temperature (SST), mixed layer depth (MLD) (the depth of the top of the thermocline), and the gradient of temperature between the surface and the MLD ("in layer gradient", INGRAD).

EFFECTS OF OCEAN THERMAL STRUCTURE ON THE PROPAGATION OF SOUND

GENERAL SOUND PROPAGATION MODEL IN RELATION TO THERMAL STRUCTURE

The sound waves, as most true wave motions, follow the SNELLIUS law, i.e. they refract towards the lower velocity of propagation. It is most appropriate to present the propagation paths in the form of sound rays which are perpendicular to the wave front.

A typical sound speed structure and a few significant sound rays are given in Fig. 1. The following features of interest are depicted in this figure: (a) the sound propagation in the surface duct, (b) the distance of the "partial shadow zone", and (c) the width and distance of the bottom bounce beam. The dependence of these features on the thermal structure were investigated, using a precision ray tracing technique (AYRES, WOLFF, CARSTENSEN and AYRES 1966) on the CDC 1604 computer. This ray tracing technique uses a time step of 1/124 second and a space step of 10 metres and includes the effects of the curvature of the earth. A ray bundle of 16° (+8° to −8°) was used corresponding roughly to the average beam width of sonars in use.

The ray traces of various thermal structure profiles (33 in number) with varying SST, MLD and INGRAD were computed. A few examples

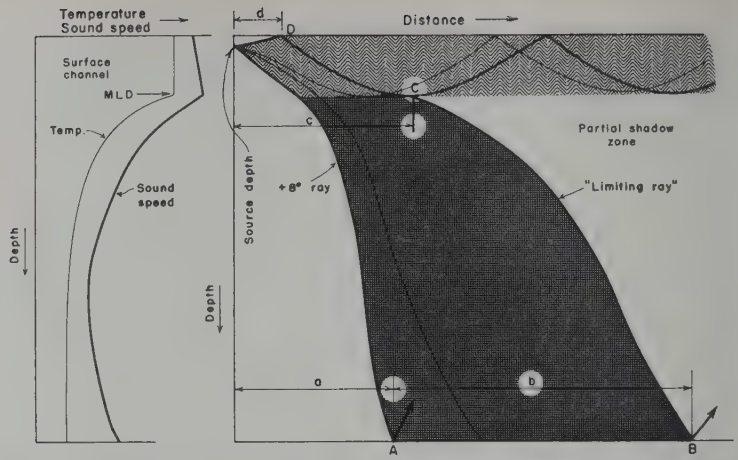

Fig. 1. A typical temperature and sound speed profile and significant sound rays.

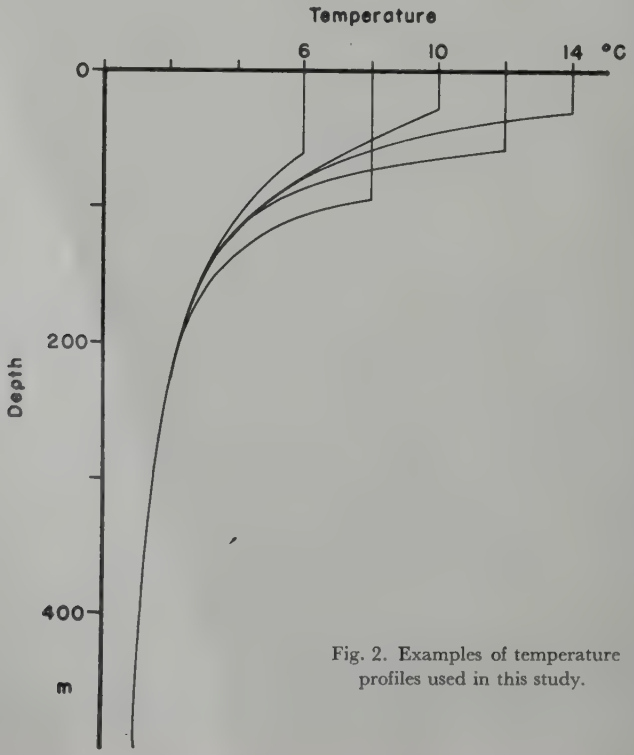

Fig. 2. Examples of temperature profiles used in this study.

of the selected profiles are shown in Fig. 2. The study of the influence of SST and MLD on the sound propagation parameters of interest was made with an isothermal layer from surface to MLD. Thus, the sound speed increases from the surface to the MLD where it reaches a maximum due to pressure effects on sound speed. Some of the nearly horizontal sound rays will become trapped in the surface mixed layer as the sound rays bend slightly towards the surface above the MLD. A separate study was made of the effects of negative temperature gradients between the surface and the MLD.

The ray tracing was computed to a maximum depth of 500 metres and to a maximum distance of 10 kilometres. The salinity was taken constant from the surface to 500 metres. The effect of salinity on sound speed is considerably smaller than that of temperature. Furthermore, it is relatively easy to ascertain the synoptic thermal structure (e.g. with bathythermograph cast) from a fishing vessel, whereas the determination of synoptic salinity structure from fishing vessels is, at present, not possible.

SEA SURFACE TEMPERATURE, MIXED LAYER DEPTH AND "IN LAYER GRADIENT" AS BASIC PARAMETERS FOR ESTIMATION OF SOUND PROPAGATION PATH IN NEAR-SURFACE LAYERS

The portion of sound energy, trapped in the surface layer and measured here in terms of the width of the trapped beam, depends greatly on the MLD (Fig. 4) and partly on source depth. However, Fig. 4 indicates that this beam width is also slightly dependent on SST. This latter dependence is mainly caused by the non-linearity of the sound speed dependence on temperature and depth (see Fig. 3).

The relation of the width of the bottom bounce beam to the SST and MLD is shown on Fig. 5. The "inner limit" (distance a on Fig. 1) is independent of MLD but dependent on SST. The relation to SST, although statistically a very good and reliable one, is, however, an indirect relation, the direct cause being the thermocline gradient and magnitude. It can be noted that if the transducer/receiver beam width is 16° and if it is horizontal, the area with a radius of a (see Fig. 1) is not sonified by such a sonar beam. This area, however, is sonified by vertical beams (such as an echo sounder beam).

The width of the bottom bounce beam (distance b) depends on depth (taken constant, 500 m in Fig. 5), SST and MLD. Again, the relation to SST is an indirect one via thermocline gradient and magnitude.

Fig. 6 presents the relations between SST, MLD and the closest point immediately below the top of the thermocline where the "partial shadow zone" starts (distance c in Fig. 1). The term "partial shadow zone" is

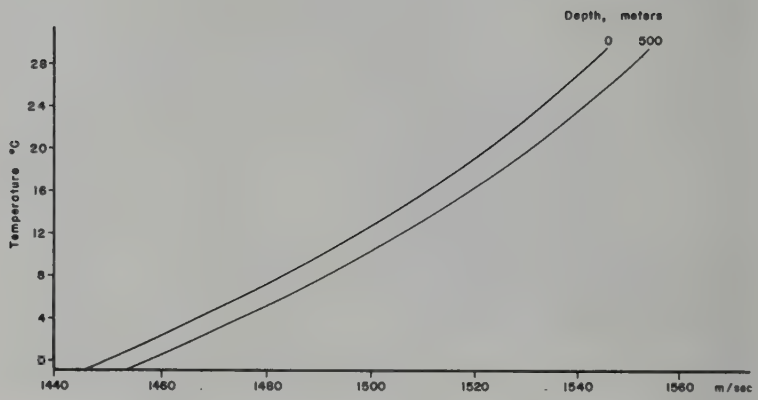

Fig. 3. Sound speed at different temperatures (0 and 500 m depth, salinity = 35‰).

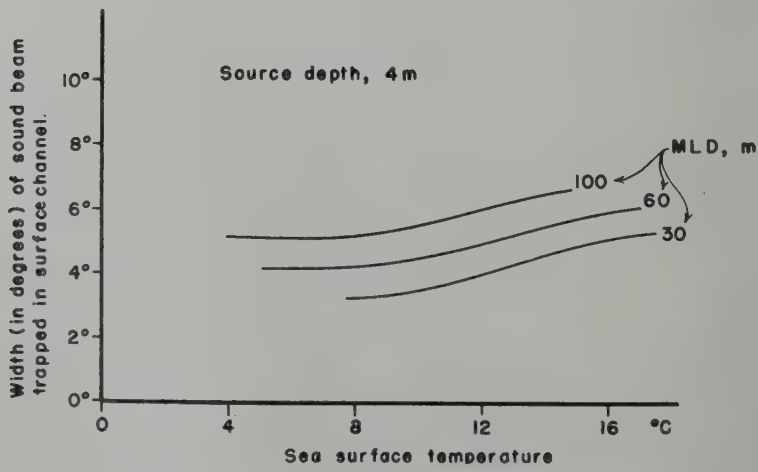

Fig. 4. Beam width of sound trapped in surface channel at different SST and MLD (source depth 4 m).

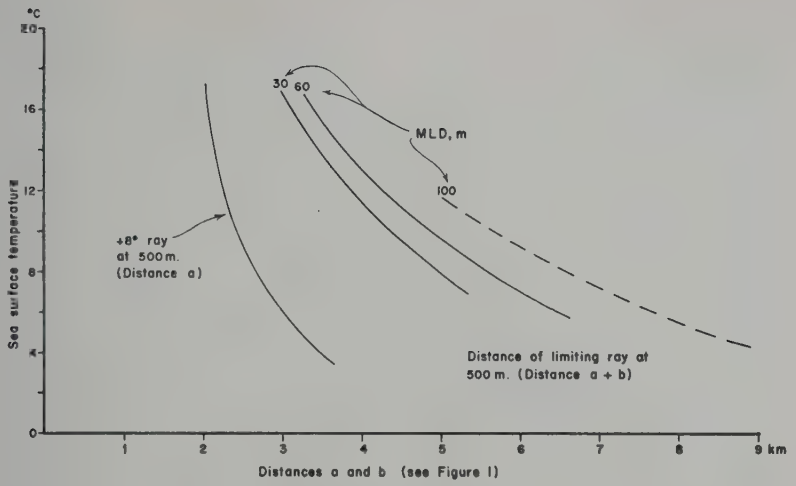

Fig. 5. Horizontal distance and width of the bottom-bounce beam in 500 m depth in relation to different SST and MLD.

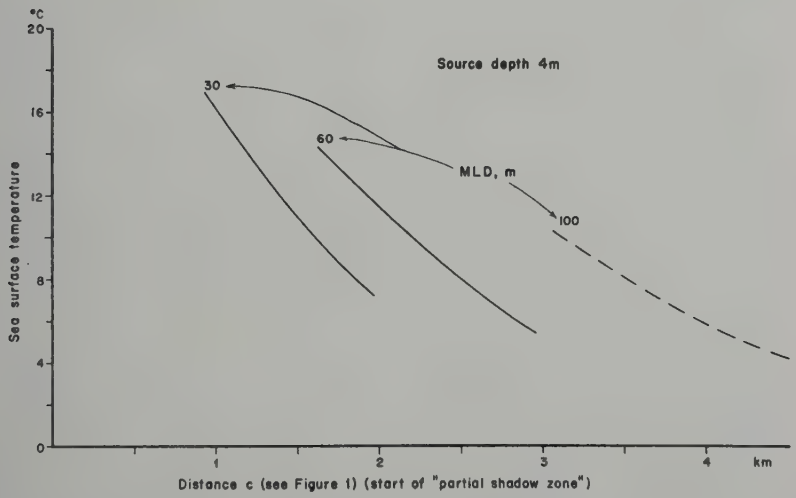

Fig. 6. Closest distance to "partial shadow zone" immediately below MLD in relation to different SST and MLD.

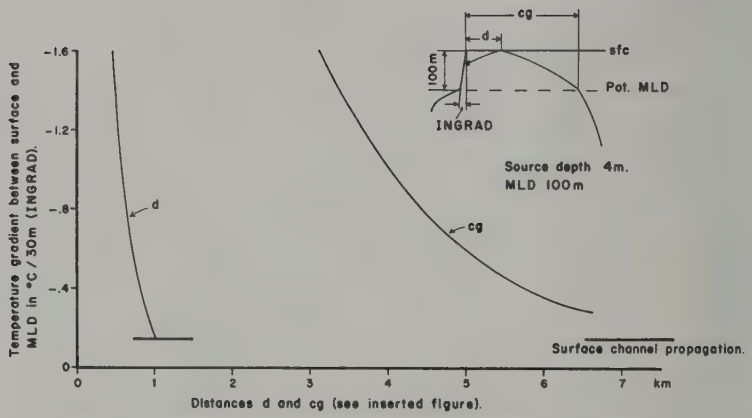

Fig. 7. Maximum grazing distance at the surface and distance at which last surface grazing ray leaves surface channel at different "in layer gradient" (INGRAD) (source depth 4 m, MLD 100 m).

used because this zone is not entirely void of sound (derived from bottom bounce and from bounce on irregular surface and irregularities in the interface (MLD)). The "distance c" is obviously greatly dependent on MLD and source depth, but also depends on SST, as Fig. 6 indicates. This latter dependence is directly caused by the sound speed change with temperature and by the non-linearities in this change (Fig. 3).

The above described relations referred to the isothermal surface mixed layer. However, this layer is not always isothermal and contains small transient thermoclines, especially during the heating season in spring and early summer. Computations with different negative temperature gradient above the top of the thermocline were made, and the results are presented in Fig. 7.

When the temperature gradient (INGRAD) in the surface layer is more negative than —0.15°C per 30 m, there is no surface channel propagation. The distance at which the last ray leaves the surface layer depends on the MLD and the INGRAD (see Fig. 7).

Finally, it is emphasized that the relations described above referred to the delineation of the sonified field. The computation of fishing sonar ranges must include propagation loss computations and other parameters, as briefly outlined in the first two chapters.

SUMMARY

1. The width of the sound beam trapped in the surface channel depends, besides on MLD and INGRAD, also on SST. The latter relation is brought about by nonlinearity in the sound speed dependence on temperature and depth (Fig. 4).
2. The bottom bounce beam width depends primarily on the temperature gradient and magnitude of change in the thermocline. With limited sonar beam width, the area near the ship below the thermocline is not accessible to horizontal beams (Fig. 5).
3. The distance to the "partial shadow zone" depends primarily on MLD, but is also affected by SST (Fig. 6).
4. If the INGRAD is more negative than —0.15°C per 30 m, there is no surface channel propagation. The distance at which the sonified field in the surface channel ends, depends on INGRAD and MLD (Fig. 7).

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DESIGN OF A SONAR FOR FISH COUNTING

By

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INTRODUCTION

Some three years ago the Marine Laboratory commenced a study of the feasibility of making population assessments by echosounder. The species of prime interest was the herring of the northern North Sea.

The study involved a review of work in progress elsewhere, a decision about the most suitable kind of equipment to use, and consideration of the statistical mathematics required for the interpretation of results. The choice of equipment, and of the resolution required, was of course influenced by the known facts about the distribution of herring.

It was felt that the counting and sizing of individual echoes would provide more information than an integration method, as it offered the prospect of classifying fish in accordance with their target strength (T decibels). To make this a practical method for routine surveys a degree of automation was required, so that the observational task aboard ship could be kept to reasonable proportions.

Since the population density of herring can be at times very high (as much as 10 or 20 per cubic metre in daylight schools) it was decided to aim for the highest degree of resolution attainable within the available funds. Our previous experience suggested that an acoustic frequency of 400 kHz was about the optimum, offering a practical range of about 150 m, and a total beamwidth of about $1\frac{1}{2}^{\circ}$, using a transducer small enough to mount in a towed body of reasonable weight, around 80 kg (Fig. 1).

EQUIPMENT

ECHOSOUNDER

A trial equipment incorporating a commercial pulse height analyser was manufactured and used from "Explorer" in July 1967 and 1968. This proved reasonably successful, and a more compact equipment is now

Contribution given in honour of Gunnar Rollefsen at his 70th birthday.

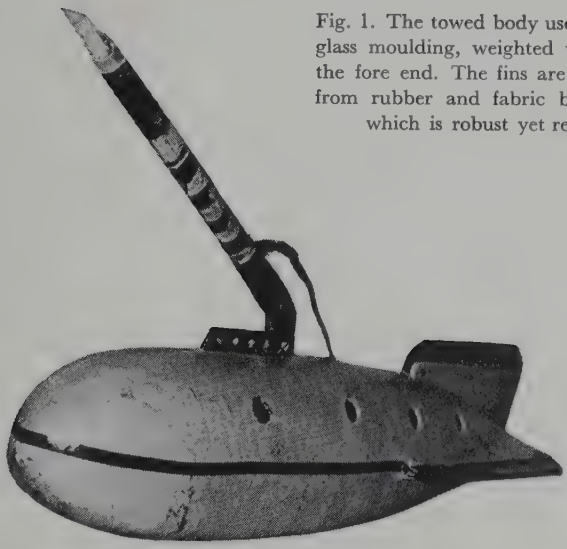

Fig. 1. The towed body used is a fibreglass moulding, weighted with lead at the fore end. The fins are constructed from rubber and fabric belt material which is robust yet resilient.

under construction, incorporating improved techniques. The principal characteristics of the new echosounder are as follows:

Frequency 400 kHz.

Transducers—circular PZT of 18 cm or 48 λ diameter.

Nominal beamwidth 0.011 radians or 0.75° half angle to 3 db point.

Range resolution—better than 15 centimetres, nominal pulse length 100 μ sec.

T.V.G. as 40 Log R $\times$ 0.18 R (R = range in metres).

Acoustic transmit power about 400 watts. Source level about 138 db ref. 1 μ bar at 1 metre.

Transducers in a towed body which also houses a preamplifier of 40 db gain.

Very low noise levels; the RMS noise referred to the transducer is about 0.1 μV.

Effective range for fish counting about 160 metres; for sea-bed echoes about 400 metres.

All timing functions are now controlled by a 100 kHz crystal oscillator. The output of this is divided by a series of 9 decades in integrated circuit form. By conventional use of inverters and gates, output pulses are derived to control transmissions, T.V.G. start and stop, and analyser functions, which will be described later. The 1 kHz decade output is used also to control the motor speed of a precision paper recorder, which acts

as a monitor on the correct working of the whole system, and also provides short-term information about targets. The transmission is derived by gating a crystal oscillator to a conventional transistor push–pull output stage.

The receive system consists at present of a preamplifier with a gain of around 40 db feeding an Eddystone radio receiver to which the time-varied gain (T.V.G.) is applied. The intermediate frequency (I.F.) output of the Eddystone receiver at 720 kHz is tailored to suit the pulse analyser, and the audio circuits left feeding a speaker which is quite distinctive in alerting the operator to fish echoes.

The T.V.G. voltage is derived as the sum of two exponential sweeps, the start and rate of both being accurately controllable.

PULSE HEIGHT ANALYZER

The analyser used is a Laben 400 channel machine, slightly modified to suit the particular application. Such analysers are adaptable to many modes of use, but we confine ourselves here to a standard procedure. Analysis begins 10 milliseconds after transmission, and sorts echoes into 20 time intervals each of 10 milliseconds duration. In other words echoes are classified into twenty depth intervals, the first being from 7.5 m to 15 m, and the last being 150 m to 157.5 m.

Echoes falling into each of these time intervals are classified into twenty amplitude channels, each of 80 millivolts amplitude, and a back-bias of 80 millivolts is applied. Thus the first amplitude channel is 80–160 millivolts, and the last amplitude channel is 1.60 to 1.68 volts. By using a logarithmic amplifier these channels can be converted to decibel levels.

At the end of a predetermined period, the analyser feeds the stored data to a teletype machine to provide both a printed record and a punched tape for subsequent computer processing. At the same time, the stored information is erased, so that after print out the sequence can be repeated.

Thus we have the potential, using a standard instrument, to make a detailed analysis of echo information.

In water less than 157 m depth, the sea-bed echo would give rise to spurious counts. Hence it is necessary to eliminate it. This general problem of sea-bed elimination (S.B.E.) was originally dealt with by stopping the analyser 3 milliseconds before the appearance of the sea-bed echo. The timing for this function was derived from the previous sea-bed echo. This is not precise enough to allow demersal fish to be counted, hence an alternative is being adopted. This is the provision of a transmitted pre-pulse at 300 kHz, which can be used in two ways.

(a) The pre-pulse is transmitted 200 μ seconds in advance of the main transmission. Receipt of the 300 kHz sea-bed echo shuts down the analyser. Thus we have an S.B.E. system allowing fish to be counted to a distance of 20 or 30 cm above the sea-bed.

(b) Where detailed analysis of the depth distribution of demersal fish is required, the pre-pulse can be made to occur 20.2 milliseconds before the main transmission. The 300 kHz sea-bed echo is now used to start the analyser, which then is swept through its time channels in 20 milliseconds instead of its standard 200 milliseconds, thus sampling a 15-metre layer above the sea-bed.

GENERATION OF SAMPLING PULSES

The pulse analyser is designed to deal with pulses of rise times less than 1 microsecond, whereas rise times of fish echoes in this case are of the order of 80 microseconds. The envelope of the echo signal thus has the characteristic of a slowly varying signal so far as the machine is concerned, and in such a case sampling pulses are required to select the instants for amplitude measurement. The principle used for this is illustrated in Fig. 2. If the incoming pulse is differentiated, a zero-crossing

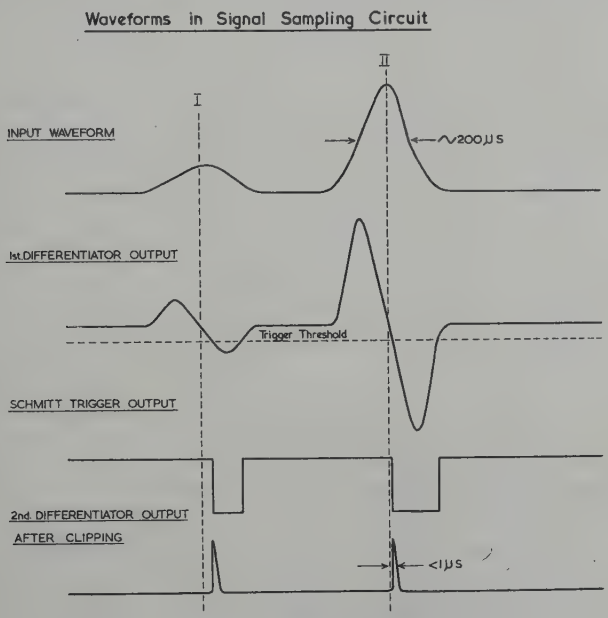

Fig. 2. Waveforms in the signal sampling circuit.

occurs very close in time to the pulse peak. If this differentiated signal is over-amplified to square it, and differentiated again, we can by selecting the appropriate polarity obtain a sampling pulse suitable to trigger the analyser, and occurring at the appropriate instant. The squaring amplifier is in fact a Schmitt trigger, whose threshold is set at a low level to avoid timing errors, as shown in I and II. It is important that this "signal selector" system should be of adequate sensitivity so that it is not itself the limiting factor in echo detection. It is desirable rather that calibrated back-bias control on the analyser should determine the minimum echo height for a count.

RECORDING MONITOR

The working of the analyser produces information pulses when an echo goes into the magnetic core store, and for instance when an echo overflows the top channel. Bearing in mind the original concept, it was desired to ensure that the working of the system could be made obvious and the information displayed immediately in a conventional form. To do this a Mufax paper recorder was employed, the speed being controlled by the same crystal clock as programmed the transmit and analysis cycles. Thus the recorder runs in synchronism with the transmissions in the usual way. It was arranged that storage of an echo by the analyser would generate a 1 millisecond marker pulse, and overflow of the top channel would produce a 7 millisecond marker pulse. Thus fish echoes counted produce small ticks, and the sea-bed echo produces a long mark. If the system is working as intended, a normal-looking recording results which is closely analogous to that of a conventional echo-sounder. It should be noted, however, that the recorder cannot be made to carry as much information as the analyser, as the range resolution on paper cannot be pushed to much less than 1 m. The analyser by contrast gives the full resolution of the acoustic system, its own internal limits in this respect corresponding to a range resolution of about one cm or less.

ANALYSIS

It is easy to predict the distribution of echo amplitudes from a known distribution of targets, but the inverse process is a little more difficult. In the treatment that follows no attempt is made to sort out all the statistical implications, a task we feel to be more appropriate to a professional mathematician. Thus we attempt here to lay down the problem, and an outline solution in such a way as to stimulate more sophisticated mathematical analysis. It will however be evident that the nature of the

directivity function is the determinant of the statistical accuracy attainable. If it were practical to produce a beam of definite angular width, at the edge of which the acoustic energy dropped from a standard value to zero sharply, then very significant results could be obtained even from small numbers of targets. However it will be well enough understood that such a situation can only be approached by the adoption of parameters much more extreme than have been contemplated here, though if a much smaller maximum range were acceptable, as it might be in a plankton counter, one could greatly improve matters in this respect.

The prime assumption made in the present treatment is that the T.V.G. has been so arranged that the echo from a small target is independent of range, i.e. allowance has been made for spreading loss and for attenuation in the medium.

Information is obtained in the form of signal levels. It is based on 20 or 50 minutes' survey, and is printed out and punched on paper tape by the teletype machine.

However the information is wanted in another form, as a distribution of target strengths.

Since the T.V.G. is a full correction, the echo of any target is independent of range. The amplitude depends only on the angular coordinates of the targets.

The essential part of the treatment is to assume some density of fish, and deduce the echo distribution that would result. We then use this to deduce density from echo distribution.

Consider any range slice lying between R_1 and R_2 in the beam, and let the solid angle be k. The volume in the range slice is

$$\int_{R_1}^{R_2} kR^2 dR = 1/3\, k\,(R_2^3 - R_1^3)$$

Thus if there be N_1 targets per cubic metre in this range slice, of target level -40 db, the number contained in the solid angle k is $1/3\, N_1 k(R_2^3 - R_1^3)$.

We now have to consider the directivity pattern of the equipment. This can be obtained theoretically by combining the transmit and receive directivities. Better, it can be obtained by direct field trial at some suitable range, e.g. 100 m. The complete way to show the results is to plot a cross-section of the beam and we may suppose this to have been done. (Fig. 3.) The levels chosen are arbitrary and have been chosen so as to include a suitable gain for our purpose. Since the beam angle is small, the area within a contour measured in $(\text{radian})^2$ corresponds to the solid angle in steradians.

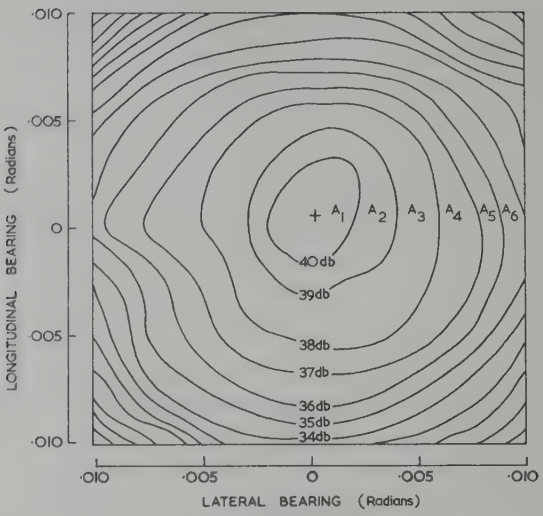

Fig. 3. Cross-section of acoustic beam pattern.

The —40 db targets will be detected only in the centre area A_1, and the echoes will be between 0 and 1 db. We call this channel 1. The number of echoes in this class is $N_1 \cdot 1/3\ k(R_2^3 - R_1^3)$ where we now know $k = A_1$.

Now consider there to be N_2 targets present of target level —39 db. These will give $N_2 \cdot 1/3\ A_2(R_2^3 - R_1^3)$ echoes in channel 1 plus

$N_2 \cdot 1/3\ A_1(R_2^3 - R_1^3)$ echoes in channel 2

—— and so on.

Suppose an eventual count in this depth slice was n_1 echoes in channel 1, n_2 in 2, n_3 in 3 and so on. Then we see that

$$\left(\frac{3}{(R_2^3 - R_1^3)}\right) \cdot n_1 = A_1N_1 + A_2N_2 + A_3N_3 \ \ldots + A_{20}N_{20}$$

$$\left(\frac{3}{(R_2^3 - R_1^3)}\right) \cdot n_2 = A_1N_2 + A_2N_3 \ \ldots + A_{19}N_{20}$$

$$\left(\frac{3}{(R_2^3 - R_1^3)}\right) \cdot n_3 = A_1N_3 \ \ldots + A_{18}N_{20} \text{ etc.}$$

giving 20 sets of equations.

A general solution can be found in the form

$$\left(\frac{R_2^3 - R_1^3}{3}\right)N_1 = B_1n_1 + B_2n_2 + B_3n_3 \ \ldots \ + B_{20}n_{20}$$

$$\left(\frac{R_2^3 - R_1^3}{3}\right)N_2 = \quad B_1n_2 + B_2n_3 \ \ldots \ + B_{19}n_{20}$$

$$\left(\frac{R_2^3 - R_1^3}{3}\right)N_3 = \quad B_1n_3 \ \ldots \ + B_{18}n_{20} \text{ etc.}$$

where the coefficients B_1, B_2 ... B_{20} are dependent only on the acoustic beam shape. A computer can put in the range corrections and print out the desired data in the form of target density as a function of target strength.

The estimate of mean density has finally to be divided by the number of transmissions.

ACCURACY

In order of importance, the accuracy of the system is dependent on (a) knowledge of the attenuation of sound in sea water, which determines the constants of the time-varied gain; (b) accuracy of determination of the beam pattern. When these are sufficiently known to give confidence, it may be worth introducing a correction for ship speed, which causes the transmit and receive beam patterns to be displaced relatively by a small angle. It must also be accepted that roll or pitching of the towed body, if accurately known, would give rise to calculable corrections.

PRELIMINARY SURVEY

A preliminary survey was carried out east of the Shetlands during August 1968. As, at this stage, the analyser output was being printed, not punched, a full analysis cannot be presented. However, some indication of the nature of the observations will be helpful. Transmissions were made every two seconds, data were recorded for twenty minutes in every half hour and printed out during the remaining ten minutes. The total number of counts in any half hour period varied enormously, from zero to over one thousand. During preliminary trials the gain was set at a level where very few counts were recorded in the highest amplitude channel, and during the survey only a very few echoes overspilled this level, indicating that the gain setting was about right for the population being sampled. Two samples of Mufax record are shown in Figs. 4 and 5, Fig. 4 showing a large mid-water school with some fish traces near the bottom in 110 m, while Fig. 5 shows a more scattered population.

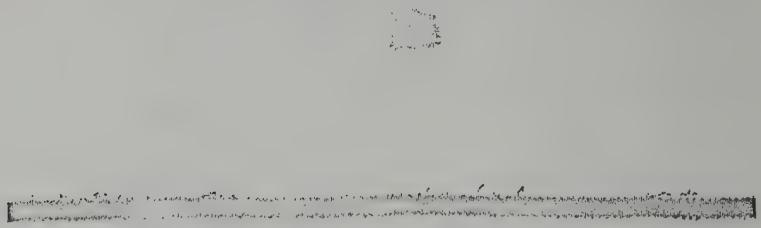

Fig. 4. Sample record from the Mufax precision recorder, used to monitor the system. The record shows a large shoal and demersal fish and covers 2 miles in 110 m depth.

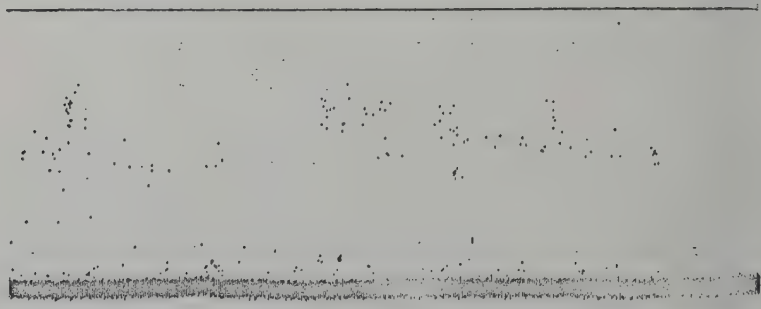

Fig. 5. Sample record from the Mufax precision recorder, used to monitor the system. The record shows scattered fish and covers 2 miles in 130 m depth.

Total counts recorded during a selected 24-hour period amounted to 845 for the region of depth of less than 52.5 m, and 6,561 for the region below 52.5 m. After applying corrections for range, this gave a pelagic fish estimate of 845 per million cubic metres for the upper zone, and 322 per million cubic metres for the deeper region. The selected period involved a north–south steam about fifty miles east of the Shetland Islands. Since paper tape was not in use at that stage, a full analysis cannot be given, nor were the various calibrations sufficiently advanced for this to be offered as a serious fish assessment.

It will be clear that a great deal of work remains to be done, in particular on transducer measurements, and in general on acoustical target strengths of fish. It appears, that the technique can give a great deal more information about pelagic fish populations and distribution than has been hitherto available.

SUMMARY

The paper described (a) A very high resolution echo-sounder, (b) A method of sorting echoes by amplitude and range, (c) A study of the analysis required to transform from distribution of echoes to distribution of targets.

Under (a) the main parameters were—frequency 400 kHz—range resolution 15 centimetres—beam angle to half-power point 0.011 radians.

The equipment for recording echoes (b) is a pulse height analyser. Echo information is stored in twenty range intervals, each subdivided into 20 categories of amplitude.

It was shown (c) that the process of determining target distribution from echo distribution can be dealt with by computer, and resolves itself into a correction for angular spread of the beam, followed by a transformation to allow for the directivity pattern. This latter transformation is equivalent to solving twenty simultaneous linear equations for each range element. The coefficients of the equations are constants for the equipment, thus the set can be solved once, and the result applied to each successive range element by a simple programme.

ACKNOWLEDGMENTS

The authors wish to express their thanks to Messrs. R. G. Lawrie, I. B. Petrie ad R. L. Craig for aid in design and construction of the equipment, and to Mr. R. Broomfield of Nuclear Enterprises Ltd., Edinburgh, for his work in modifying the pulse analyser.

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THE RELATIONSHIP BETWEEN ARCTIC AND COASTAL COD IN THEIR IMMATURE STAGES ILLUSTRATED BY FREQUENCIES OF GENETIC CHARACTERS

By

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INTRODUCTION

The cod, *Gadus morhua* L., which inhabit the Norwegian coast and the Barents Sea, form two genetically separate populations (Møller 1968a). In spite of the simultaneous spawning in the same areas the two groups of cod have significant differences in frequency of the haemoglobin *Hbl*[1] allele (Sick 1965) and of the blood types A and E (Møller 1967). The investigations did not record possible gene flow from one gene pool to another, implying that the Arctic and the coastal cod should be regarded as two sibling species (Møller 1968b).

The present paper describes the variation of the *Hbl*[1] allele and the blood type E frequencies of samples of immature cod, which have been collected inshore and offshore at the bottom along the Norwegian coast and in the Barents Sea. Since Arctic and coastal cod are characterized by certain frequencies of these characters (Møller 1968a), this variation also gives expression for the relationship between immature Arctic and coastal cod.

Portions of this material have been published previously either as a part of other investigations (Frydenberg, Møller, Nævdal, and Sick 1965; Møller 1967) or as a preliminary report (Møller, Nævdal and Valen 1967).

MATERIAL AND METHODS

The material consists of two main parts: fourteen samples of cod fry, totalling 914 specimens, from the Vestfjord, Troms, and Finnmark area (Table 1, Fig. 1); and forty-eight samples of young cod, of which the

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Contribution given in honour of Gunnar Rollefsen at his 70th birthday.

Table 1. Date, locality and number of specimens of, and gear used for collected cod fry samples.

Sample No.	Date	Locality	Number of specimens	Gear
1	4 Oct. 63	Øksfjorden	60	Shore seine
2	4 Oct. 63	Øksfjorden	65	Shrimp-trawl
3	27 Oct. 64	Øksfjorden	60	Shrimp-trawl
4	3 Oct. 63	Gausvik, Vågsfjorden	81	Shore seine
5	28 Oct. 64	Gausvik, Vågsfjorden	73	Shore seine
6	3 Oct. 63	Rolla, Vågsfjorden	77	Shrimp-trawl
7	28 Oct. 64	Rolla, Vågsfjorden	80	Shrimp-trawl
8	5 Oct. 63	Eidsfjorden	22	Shore seine
9	5 Oct. 63	Eidsfjorden	84	Shrimp-trawl
10	9 Oct. 63	Ulsfjorden	85	Shore seine
11	9 Oct. 63	Ulsfjorden	67	Shrimp-trawl
12	8 Oct. 63	Altafjorden	68	Shore seine
13	8 Oct. 63	Altafjorden	15	Shrimp-trawl
14	1 Nov. 64	Varangerfjorden	77	Shrimp-trawl

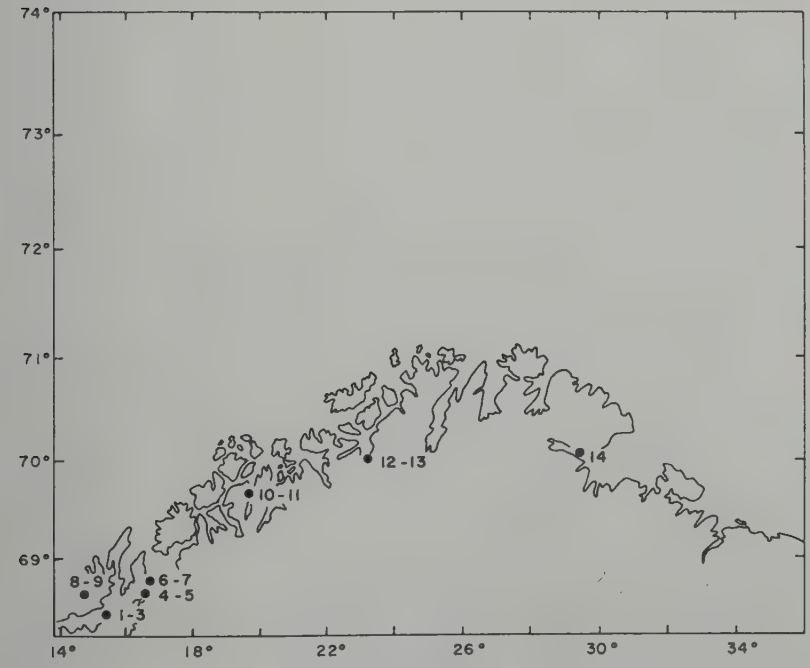

Fig. 1. The location of capture of fourteen cod fry samples.

Table 2. Date, locality and number of specimens of, and gear used for collected samples of young cod.

Sample No.	Date	Locality	Number of specimens	Gear
1	4 Oct. 63	Øksfjorden	57	Shrimp-trawl
2	27 Oct. 64	Øksfjorden	80	Shrimp-trawl
3	25 Oct. 65	Øksfjorden	109	Shrimp-trawl
4	3 Oct. 66	Øksfjorden	115	Shrimp-trawl
5	3 Oct. 63	Gausvik, Vågsfjorden	28	Shore seine
6	26 Oct. 65	Rolla, Vågsfjorden	26	Shrimp-trawl
7	28 Oct. 65	Målsnes, Malangen	85	Shrimp-trawl
8	30 Sept. 66	Målsnes, Malangen	97	Shrimp-trawl
9	10 Oct. 63	Tromsø	191	Trap-net
10	9 Oct. 63	Breivik, Ulsfjorden	20	Shore seine
11	7 Oct. 63	Breivik, Ulsfjorden	156	Shrimp-trawl
12	11 Nov. 64	Breivik, Ulsfjorden	115	Shrimp-trawl
13	16 Sept. 66	Breivik, Ulsfjorden	120	Shrimp-trawl
14	29 Oct. 65	Grøtnes, Ulsfjorden	59	Shrimp-trawl
15	28 Sept. 66	Årøy, Kvenangen	120	Shrimp-trawl
16	29 Sept. 66	Rødøy, Kvenangen	114	Shrimp-trawl
17	8 Oct. 63	Bosekop, Altafjord	156	Shrimp-trawl
18	30 Oct. 64	Bosekop, Altafjord	95	Shrimp-trawl
19	30 Oct. 65	Bosekop, Altafjord	39	Shrimp-trawl
20	19 Sept. 66	Bosekop, Altafjord	120	Shrimp-trawl
21	28 Feb. 66	Sørøya N 71° 03′, E 23° 31′	98	Trawl
22	2 Nov. 65	St. Tamsøy, Porsangerfjorden	173	Shrimp-trawl
23	16 Mar. 66	St. Tamsøy, Porsangerfjorden	119	Shrimp-trawl
24	20 Sept. 66	St. Tamsøy, Porsangerfjorden	120	Shrimp-trawl
25	27 Sept. 66	Svaerholt, Porsangerfjorden	118	Shrimp-trawl
26	6 Nov. 64	Mårøy, Laksefjord	96	Shrimp-trawl
27	5 Nov. 64	Kjeldneset, Tanafjord	120	Shrimp-trawl
28	21 Sept. 66	Kjeldneset, Tanafjord	119	Shrimp-trawl
29	26 Sept. 66	Losvik, Tanafjord	120	Shrimp-trawl
30	14 Mar. 63	Tanasnaget N 71° 06′, E 29° 00′	115	Trawl
31	20 Apr. 64	Tanasnaget N 71° 00′, E 29° 04′	40	Trawl
32	2 Mar. 66	Tanasnaget N 71° 01′, E 29° 06′	118	Trawl
33	15 Jan. 67	Tanasnaget N 70° 58′, E 28° 59′	120	Trawl
34	12 Nov. 65	Makkaur	119	Long line
35	2 Nov. 64	V. Jacobselv, Varangerfjorden	93	Shrimp-trawl
36	23 Sept. 66	Vadsø, Varangerfjorden	118	Shrimp-trawl
37	16 Jan. 67	Kiberg, Varangerfjorden	120	Trawl
38	4 Mar. 66	Malangsgrunnen N 69° 51′, E 16° 42′	97	Trawl
39	21 Nov. 64	Malangsgrunnen N 70° 00′, E 17° 10′	79	Trawl
40	19 Nov. 64	Bear Island N 73° 55′, E 18° 15′	133	Trawl
41	28 Feb. 64	Nordkapp Bank N 72° 12′, E 24° 25′	123	Trawl
42	1 Mar. 66	Nordkapp Bank N 71° 55′, E 25° 10′	120	Trawl
43	20 Apr. 64	Nordkyn N 71° 14′, E 27° 55′	90	Trawl
44	18 Jan. 67	East Bank N 70° 16′, E 32° 25′	117	Trawl
45	12 Mar. 63	East Bank N 70° 06′, E 33° 45′	138	Trawl
46	13 Mar. 63	Skolpen Bank N 70° 54′, E 34° 00′	80	Trawl
47	10 Mar. 63	Skolpen Bank N 70° 10′, E 34° 50′	150	Trawl
48	26 Jan. 67	Skolpen Bank N 71° 21′, E 35° 31′	120	Trawl

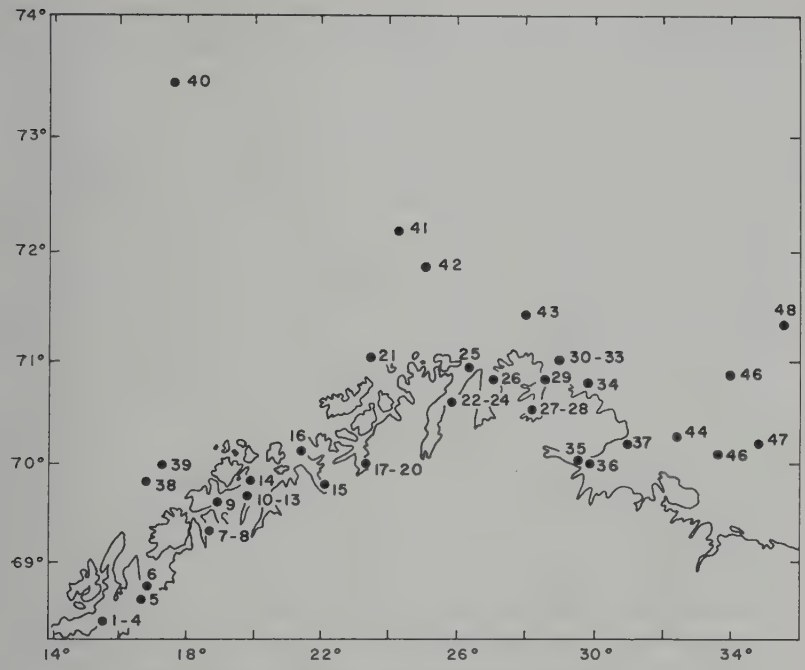

Fig. 2. The location of the forty-eight sampling stations of immature cod.

majority were from three to six years old, totalling about 5,000 specimens, from different localities in northern Norway and in the Barents Sea (Table 2, Fig. 2).

Both in Table 1 and 2 the samples are listed in geographical order from south to north and east. In Table 2 the samples from the coast are presented first and then the samples from the coastal banks and the sea. Samples taken from the same fjord are listed after locality in order from the bottom to the mouth of the fjord.

In addition to date, locality, and the total numbers of specimens in each of the samples, the tables also give information about the fishing gear used. Most of the fish were caught with the help of fishery research vessels, except for the fish caught by trap-nets and the fish in sample 34 (Table 2), which were caught by professional fishermen.

During trawling and long line fishing the depths were recorded by an echo sounder, and the approximate mean depth of the different sampling localities are given in Table 3 and 4. In the same tables the depths for the shore seine and the trap-net fishing are estimated as 2 and 15 m, respectively.

The fry blood specimens were acquired from live fish by cutting the tail, while the other blood specimens were obtained by heart puncture of live cod. The handling of the specimens, the method used in haemoglobin determinations, the blood grouping technique, and the explanation of the nomenclature used in this paper, have been described elsewhere (Sick 1965; Møller 1967). However, the blood type E frequency of nine samples, collected in 1963, was not determined due to lack of antisera at that time.

All specimens were analysed at the Institute of Marine Research, Bergen, except for the samples 32 to 35 which were sent to the Institute of Genetics, Copenhagen, where the electrophoresis was carried out (Frydenberg *et al.* 1965).

RESULTS

THE VARIATION OF THE FREQUENCY OF THE HbI¹ ALLELE IN SAMPLES OF COD FRY

Table 3 gives the distribution of the haemoglobin patterns, the frequency of the *HbI*¹ allele (q^1), and the depth of the cod fry samples. The frequencies of the samples vary between .088 (sample 7) and .432 (sample 8), and the frequencies differ significantly among samples taken in the same fjord (samples 1–3, 4–7, and 8–9) and in the same year (samples 4

Table 3. The distribution of the haemoglobin patterns, the frequency of the *HbI*¹ allele (q^1), and the depth of the cod fry samples.

Sample	*HbI*¹/*HbI*¹ homozygotes	*HbI*¹/*HbI*² heterozygotes	*HbI*²/*HbI*² homozygotes	Total of rare types	q^1	Depth of sample in meter
1	4	19	37	0	.225	2
2	4	22	39	0	.231	200
3	3	14	43	0	.167	200
4	8	19	54	0	.216	2
5	7	32	34	0	.315	2
6	0	15	62	0	.097	300
7	2	10	68	0	.088	240
8	4	11	7	0	.432	2
9	4	36	44	0	.262	250
10	6	29	50	0	.241	2
11	7	28	32	0	.313	125
12	9	25	34	0	.316	2
13	2	6	7	0	.333	70
14	3	21	52	1	.175	200

and 6, 5 and 7, and 8 and 9). The differences between these pair of samples from the same fjord are similar with high values of q^1 in shallow water and with low values in deep water.

However, the frequencies have about the same value in the samples 1 and 2, or the difference is contrary with slightly higher values in deep water in the samples 10 and 11, and 12 and 13. Regarding the difference in depth between the samples 11 and 13, and the samples 2, 3, 6, 7, and 9, the main impression is that the frequency of the *HbI*^{1} allele varies to a certain degree with the depth; the lowest values being in deeper water.

This relationship is supported further by treating the samples as grouped data. The depth versus the mean frequency of the samples belonging to the same 50 m class is plotted in Fig. 3. Only the frequencies between 51 and 150 m do not appear to fit in the diagram of correlation between depth and frequency of the *HbI*^{1} allele.

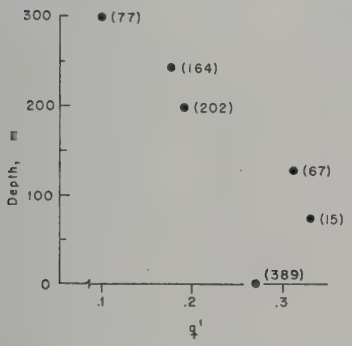

Fig. 3. Relationship between frequencies of the *HbI*^{1} allele (q^1) in in samples of cod fry and sampling depths. Figures in brackets represent the number of specimens.

THE VARIATION OF THE FREQUENCIES OF THE HbI^1 *ALLELE AND THE BLOOD TYPE E IN SAMPLES OF YOUNG COD*

The distribution of the haemoglobin patterns, the values of q^1, and of the frequency of the blood type E (p^E), together with the depth of the collected samples of young cod are listed in Table 4.

In Figs. 4 and 5 the values in samples from different localities of q^1 and p^E, respectively, are represented on a map of northern Norway and the Barents Sea. In localities which in Table 4 are shown with two or more samples, the values on the maps represent the means.

The highest values both of q^1 and p^E are found inshore (Figs. 4 and 5), whereas mostly all of the values in samples from the banks appear to be comparatively low. In most of the fjords with more than one sample the

Table 4. The distribution of the haemoglobin patterns, the frequencies of the *HbI*^{1} allele (q^1) and the blood type E (p^E), and the depth of the samples of young cod.

Sample	*HbI*^{1}/*HbI*^{1} homo-zygotes	*HbI*^{1}/*HbI*^{2} hetero-zygotes	*HbI*^{2}/*HbI*^{2} homo-zygotes	Total of rare types	q^1	p^E	Depth of sample in meter
1	4	19	34	0	.237	—	200
2	7	20	48	5	.216	.385	200
3	5	31	72	1	.188	.426	200
4	6	33	70	6	.196	.487	200
5	2	13	13	0	.304	—	2
6	1	6	18	1	.154	.269	240
7	3	20	62	0	.153	.476	200
8	5	40	52	1	.255	.674	110
9	19	83	88	1	.317	.917	15
10	2	7	11	0	.275	—	2
11	9	42	105	0	.192	—	115
12	4	38	70	3	.200	.708	110
13	1	23	96	0	.104	.458	120
14	4	17	38	0	.212	.568	175
15	6	37	76	1	.204	.508	110
16	1	18	89	6	.088	.343	295
17	9	61	86	0	.253	—	70
18	3	35	57	0	.216	.637	70
19	1	10	27	1	.154	.645	70
20	3	45	70	2	.213	.825	70
21	6	23	69	0	.179	.155	220
22	6	44	122	1	.162	.606	210
23	1	32	86	0	.143	.419	230
24	5	34	79	2	.183	.592	230
25	1	25	86	6	.114	.283	230
26	5	10	80	1	.104	.152	220
27	3	23	92	2	.121	.432	175
28	4	30	82	3	.160	.310	180
29	1	22	96	1	.100	.263	310
30	3	26	86	5	.133	—	290
31	0	9	31	0	.113	.233	220
32	3	22	89	4	.119	.164	220
33	5	28	85	2	.158	.383	100
34	2	29	87	1	.139	.187	215
35	2	31	56	4	.188	.641	200
36	1	26	91	0	.119	.244	230
37	7	39	72	2	.221	.368	110
38	1	16	80	0	.093	.208	260
39	5	19	55	0	.184	.575	220
40	3	31	90	9	.139	.101	250
41	2	23	98	0	.110	.048	265
42	1	23	96	0	.104	.112	255

Table 4 (continued).

Sample	HbI^1/HbI^1 homo-zygotes	HbI^1/HbI^2 hetero-zygotes	HbI^2/HbI^2 homo-zygotes	Total of rare types	q^1	p^E	Depth of sample in meter
43	3	14	73	0	.111	.097	250
44	5	21	90	1	.132	.068	180
45	1	21	136	2	.072	—	220
46	1	14	63	2	.100	—	180
47	0	25	124	1	.083	—	230
48	1	17	102	0	.079	.100	190

sample with the lowest value of q^1 and p^E is found near the mouth of the fjord:

Vågsfjorden	q^1: .304 and .154	p^E: —
Ulsfjorden	.173 and .212	.360 and .343
Kvenangen	.204 and .088	.299 and .189
Porsangerfjorden	.163 and .114	.330 and .154
Tanafjorden	.140 and .100	.215 and .141
Varangerfjorden	.188 and .119	.401 and .130

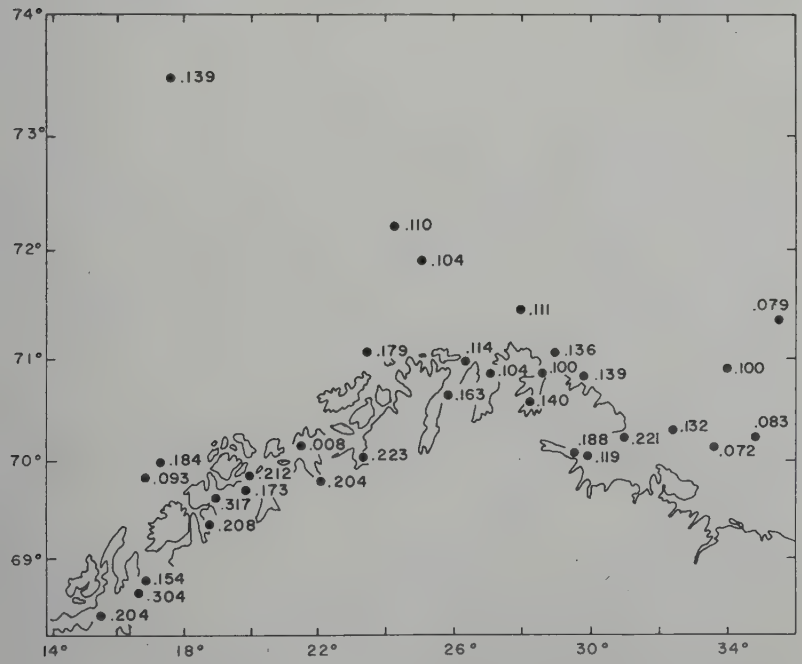

Fig. 4. The frequencies of the HbI^1 allele in the different sampling localities.

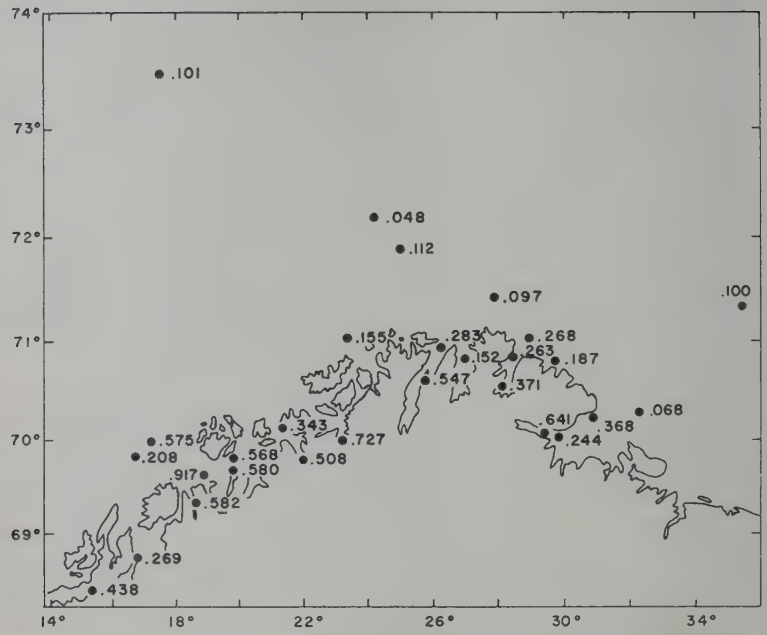

Fig. 5. The frequencies of the blood type E in the different sampling localities.

However, the figures contain more frequencies which do not fit in this general pattern, in Fig. 4 for instance, the values .212, .179, .141, and .225; and in Fig. 5 the values .917, .268, and .368. Therefore, the values of q^1 and p^E according to the depth of the sample are plotted in Figs. 6 and 7, respectively. Incidentally, the samples collected inshore and the samples within the coastal locality form four different groups as indicated on the figures.

Both in Figs. 6 and 7 the frequencies are decreasing with increasing depth. Although there are large variations from one sample to another, the values of the estimated means in each of the groups both for q^1 and p^E are decreasing continually with the values .312 and .920, respectively, near the surface to .109 and .300 at 300 m. The decline in the values of the frequencies appears greatest in the first 100 m.

The values of q^1 and p^E in samples from the sea are low (Figs. 6 and 7). Only one sample (sample 39) has intermediate values of q^1 and p^E, while the others have as low or lower values than the samples collected inshore on corresponding depth.

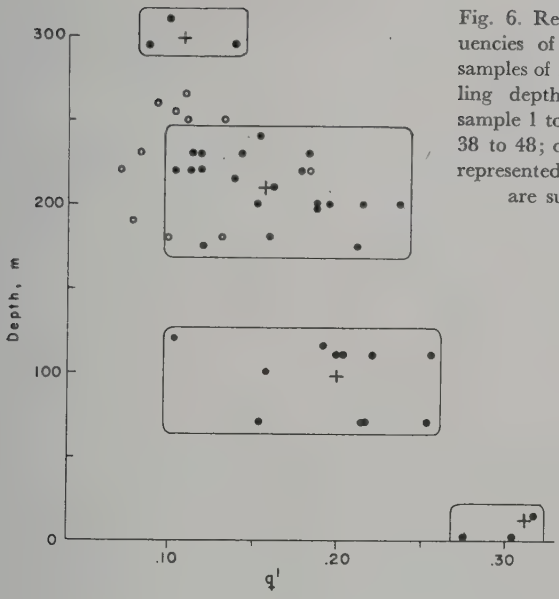

Fig. 6. Relationship between frequencies of the *Hbl*^{1} allele (q^1) in samples of immature cod and sampling depths. Legend: Black dots, sample 1 to 37; open circles, samples 38 to 48; crosses, means of samples represented by black dots and which are surrounded by a line.

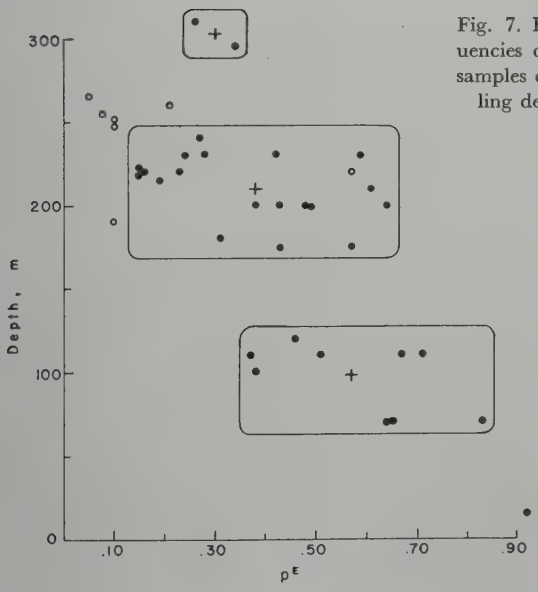

Fig. 7. Relationship between frequencies of the blood type E (p^E) in samples of immature cod and sampling depths. Legend: See Fig. 6.

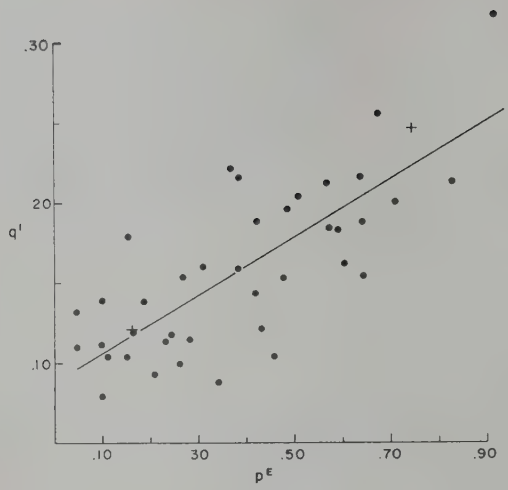

Fig. 8. Relationship between frequencies of HbI^1 allele (q^1) and frequencies of the blood type E (p^E) in the samples. Legend: Black dots, values of the samples; regression line, $y = .089 + .179\ x$; crosses, mean values of the spawning groups of Arctic and coastal cod.

The value of q^1 according to the value of p^E in the same sample are plotted in Fig. 8, together with values representing spawning groups of Arctic and coastal cod in the Vestfjord and north to the Laksefjord (Møller 1968a).

Here too there are large variations from one sample to another. However, the values correlate (correlation coefficient .77), and the data fits a straight regression line ($y = .089 + .179x$; linear regression coefficient $= .179$, highly significant $P > .01$). The mean values of the Arctic cod spawning groups fit this line, while the values of the coastal spawning groups are slightly different.

THE DISTRIBUTION OF THE HAEMOGLOBIN PATTERNS

Tables 2 and 4 list the haemoglobin patterns, the homozygotes HbI^1/HbI^1 and HbI^2/HbI^2; and the heterozygote HbI^1/HbI^2, in the cod fry and young cod samples, respectively. The total numbers of individuals in several of the samples are low, and the observed numbers of the different patterns of the individual samples in the tables deviate slightly from the expected numbers calculated from the Hardy-Weinberg law of genotype distributions in large random mating populations. However, by treating the samples in larger units it is possible to detect unconformity. The observed and expected distributions of the haemoglobins in cod fry is not in accordance:

	HbI^1/HbI^1	HbI^1/HbI^2	HbI^2/HbI^2
obs.	63	287	564
exp.	46.6	319.7	547.7

$\chi^2 = 9.561$; d.f. $= 1$; $P < .005$

Similarly, the samples collected inshore or on localities near the coast (samples 1 to 37) of young cod do not fit the Hardy-Weinberg law:

	HbI^1/HbI^1	HbI^1/HbI^2	HbI^2/HbI^2
obs.	150	1051	2633
exp.	118.8	1112.0	2603.2

$\chi^2 = 11.881$; d.f. $= 1$; $P < .005$

DISCUSSION

The main purpose of the present study is to investigate the relationship between Arctic and coastal cod in their immature stages by the variation of the frequencies of the HbI^1 allele and of the blood type E.

Due to the sampling gear the report is restricted to cod staying near or at the bottom of the sea.

The significant differences found between the observed and the expected numbers both of samples of cod fry and of young cod, demonstrate that the samples were collected from two or more genetically separated populations.

The values of q^1 and p^E correlate (Fig. 8, page 230). The estimated values appear to represent different mixtures of individuals from two distinct populations. The mean values for Arctic cod spawning groups fit in this correlation, while the values of coastal cod spawning groups have slightly higher values of q^1 for corresponding values of p^E. Rather than sampling error the reason for this is that the two groups of samples represent genetic diversity in the coastal cod in that area. While the values of the spawning groups mostly represent samples from the Vestfjord area, the values of young cod represent samples caught in different localities all over northern Norway.

In spawning groups of Arctic and coastal cod in the Vestfjord and north to the Laksefjord the mean frequencies of the HbI^1 allele were .121 and .247, respectively; and of the blood type E .162 and .722 (Møller 1968a). The specimens in these spawning groups were classified as Arctic and coastal cod according to the otolith type (Rollefsen 1933), however, otolith types are not a well-defined character. Therefore, the actual values of the Arctic cod groups are somewhat lower than these estimated values, while those values for the coastal cod groups are higher.

The low values of q^1 and p^E in a sample signify a high percentage of Arctic cod, while relatively high values of q^1 and p^E represent a high percentage of coastal cod.

Both the values of q^1 in cod fry samples and the values of q^1 and p^E in samples of young cod were decreasing with increasing depth (Figs. 3, 6 and 7). Although there are large variations from one sample to another, these variations are probably caused by the large geographical differences in sampling localities, both in latitude and in distance from the shore. All localities in the sampling area are not given equal representation. Shallow water east of the Altafjord is poorly represented. The reason for the large drop in frequencies both of q^1 and p^E in the first hundred meters is probably due to inadequate sampling. However, the coastal cod appear to prefer the shallow waters at the coast, while the deep water are prefered by the Arctic cod; an apparent feature which is also characteristic of first year cod in late autumn.

Only one of eleven samples collected from the sea appears to contain a high percentage of coastal cod (sample 39) (Figs. 4 and 5), although the depths of these samples were not deeper than the sampling depths inshore or near the coast (Figs. 6 and 7). The frequencies of the samples show that the samples primarily consist of Arctic cod. Thus, the Arctic cod is found in the open sea, while the coastal cod strain is restricted to the coastal waters.

Despite the restricted area of sampling and the limited number of samples it is convincingly demonstrated that the relative strength of Arctic and coastal cod in northern Norway and the Barents Sea appear to depend on depth and distance from the shore.

The result confirms the results of previous studies concerning the distribution of Arctic and coastal cod, such as tagging experiments and determination of the otolith types (Hylen 1964 and 1967; Sætersdal 1956).

Differences found previously between the adult stages (Møller 1968a) are supported by the different environmental preferencies demonstrated here in the immature stages. There is every reason now to regard the two cod forms as two sibling species.

SUMMARY

The frequencies of the *Hbl*^{1} allele and of the blood type E are recorded for samples of cod fry and of young cod at different localities in northern Norway and the Barents Sea.

Using the frequencies as an expression for the relationship between Arctic and coastal cod it is demonstrated that the relative strength of the

two cod forms appear to depend on depth and distance from the shore. The coastal cod prefer the shallow waters at the coast, while the open sea and deeper waters both offshore and inshore are prefered by the Arctic cod; thus, the two cod forms are regarded as sibling species.

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THE LOGARITHMIC SERIES AND THE LOGNORMAL DISTRIBUTION APPLIED TO BENTHIC INFAUNA FROM PUGET SOUND, WASHINGTON, U S A [1]

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INTRODUCTION

Collections from natural communities of organisms are characterized by unequal abundances of the various species, and several mathematical models have been proposed to represent the distribution of specimens among the species (Taylor 1953, Williams 1964). Two of the most frequently used models are the logarithmic series (Fisher, Corbett and Williams 1943) and the lognormal distribution (Preston 1948). The present paper is an attempt to test the validity of these models for communities of benthic organisms.

R. A. Fisher demonstrated that the negative binomial distribution could be applied to the frequency distribution of species abundances in samples from natural communities where the species were distributed randomly and the abundances of the various species were distributed in accordance with a Gamma-function. The proportion of species with abundance n in a sample is then expressed by:

$$P_{(n)} = \frac{(k + n - 1)!\, p^n}{(k-1)!\, n!\, (1 + p)^{k+n}}$$

where p is a parameter related to the sample size and k is an inverse measure of the variability in the abundances of the species. When applied to a collection the zero term may be omitted, since no information is available about the number of species present in the community but not included in the sample. Furthermore, the range of species abundances is

[1] Contribution No. 505, Department of Oceanography, University of Washington.

Contribution given in honour of Gunnar Rollefsen at his 70th birthday.

normally so large that k becomes nearly zero. Thus, by omitting the zero term and setting $k = 0$, and by substituting α for $1/(k - 1)!$ and x for $p/(1 + p)$ in the formula for the negative binomial distribution, FISHER arrived at the logarithmic series:

$$P_{(n)} = \alpha x^n/n$$

where $P_{(n)}$ is the proportion of species in the sample with n specimens. The relationship between number of species (S) and number of specimens (N) in the logarithmic series is:

$$S = \alpha \ln\left(1 + \frac{N}{\alpha}\right)$$

Total number of specimens in replicate samples from a community satisfying the logarithmic series will be distributed according to the negative binomial distribution and total number of species according to a POISSON-series (QUENOUILLE 1949). KENDALL (1948) showed that the logarithmic series could originate from various types of population growth, and a comprehensive account of the application of the logarithmic series to various aspects of quantitative biology is given by WILLIAMS (1964).

PRESTON (1948) questioned two consequences of the logarithmic series model, namely, that species with few specimens in a community are more numerous than species with intermediate abundances, and that no upper limit to the number of species is defined. He stated that the number of species is limited, and that it is not reasonable to expect that a major part of the species are of very low abundance; in reality the majority of the species are of intermediate abundance. PRESTON showed that the distribution is normal when the abundances are grouped in geometric classes differing by a factor of two, i.e., the distribution is lognormal. However, if a collection is small compared to the total number of species present in the community the distribution is a truncated lognormal; in such situations many of the species appear to be rare and the data fit a logarithmic series. By doubling the sample size the mode of the lognormal distribution shifts to one higher class and the distribution thus becomes less and less truncated with increasing sample size.

WILLIAMS (1953) agreed that the lognormal distribution often is preferable to the logarithmic series; however, he found that classes differing by a factor of three are better, because by PRESTON's method half of the number of species with two specimens are included in the first class and the other half in the second class. By WILLIAMS' $\times 3$ classes the species in the first class have one specimen, in the second class two to four, in the

third class five to thirteen, and in the fourth class fourteen to forty specimens, such that the midpoints of the classes are one, three, nine and twenty-seven specimens.

MATERIALS AND METHODS

The present material was collected quarterly (seven cruises) during 1963–64 at eight stations in Puget Sound in from five to ten replicate samples with a 0.1 m^2 van Veen grab (Lie 1968). All the polychaetes, crustaceans, lamellibranchs and echinoderms from the first two cruises (January–February and April–May 1963) were identified and counted; in the samples from August and November the polychaetes were identified only from stations 2 and 7; in the samples from 1964 (three cruises) polychaetes were not identified. Therefore, the logarithmic series has been applied only to the data from the two first cruises when the number of species was sufficiently high for meaningful plotting of the first ten classes of the series (species with from one to ten specimens).

The logarithmic series was fitted by finding x from table 146, page 308, in Williams (1964), and α was calculated from the formula:

$$\alpha = N(1-x)/x$$

The logarithmic series can be fitted when x and α are known (page 235). The deviation of the logarithmic series from observed frequencies was estimated by the formula:

$$D = \left[\sum_{i=1}^{n} (\log A_i - \log B_i)^2/n\right]^{1/2}$$

where A_i is the observed frequency, B_i the frequency expected from the logarithmic series, and n the number of classes.

The lognormal distribution was tested by plotting the cumulative percentage of the $\times 3$ classes on logarithmic probability paper; a lognormal distribution is represented by a straight line on such paper (Aitchison and Brown 1957).

The Shannon–Wiener function of information theory (Shannon and Weaver 1963):

$$H = -\sum_{i=1}^{S} p_i \log_2 p_i$$

is a measure of the complexity of an animal community; the more similar the abundances of the various species and the higher the number of species, the higher the diversity of the community as measured by the

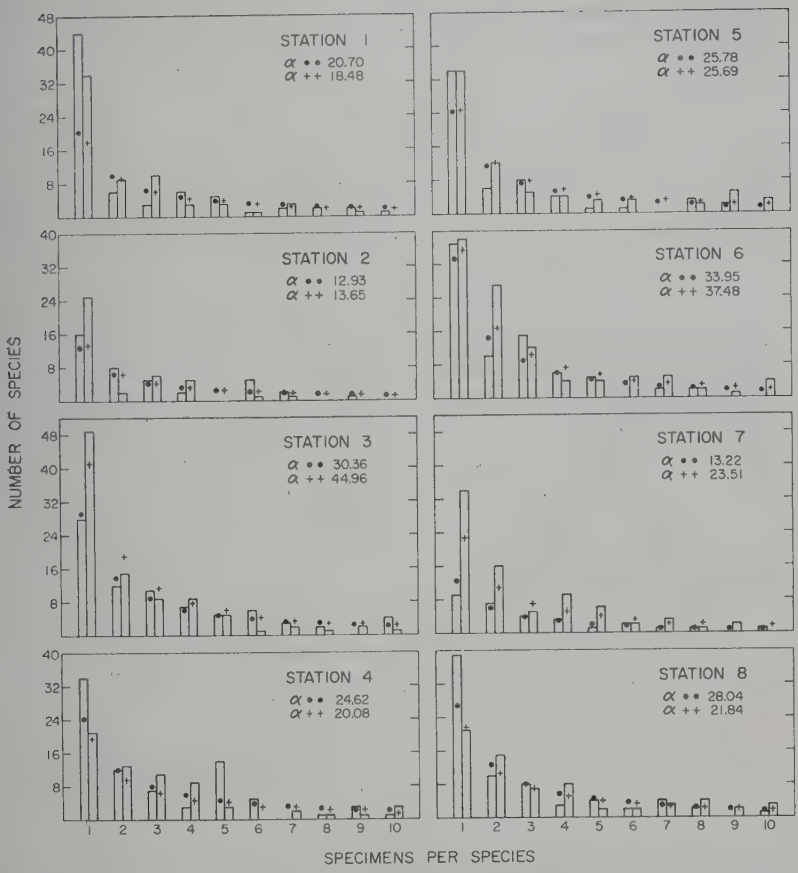

Fig. 1. Observed frequencies of specimens per species (bars) and frequencies expected from the logarithmic series in January–February (dots) and April–May (crosses) 1963 of benthic infauna from eight permanent stations in Puget Sound.

formula. The relative diversity (H_r) or "evenness" (Pielou 1966) is the ratio between the observed diversity and the maximum diversity the community could contain, i.e., if all the species were equally abundant:

$$H_r = H/H_{max} \; (H_{max} = \log_2 S)$$

Thus the relative diversity represents only the distribution of specimens among the species and is unaffected by variation in the total number of species in a sample. Shannon and Weaver (1963) defined redundancy as one minus the relative information, and the redundancy for a com-

munity of organisms is therefore a measure of the level of dominance in the community. Redundancy expressed in percent by the formula:

$$R = 100(1 - H_r)$$

has therefore been used in the present paper as a measure of the dominance of the faunal assemblages in Puget Sound.

RESULTS AND DISCUSSION

THE LOGARITHMIC SERIES

Fig. 1 shows the observed frequencies and the frequencies expected from the logarithmic series of species with from one to ten specimens in the samples from the eight stations in Puget Sound during January–February and April–May 1963. There is generally a reasonably good fit, but in seven of the sixteen cases the discrepancy between observed and expected frequencies was larger than could be expected when tested by a Chi^2 test (Table 1). Since the logarithmic series were fitted by determining two parameters, x and α, the degrees of freedom in the Chi^2 tests equal the number of classes minus two.

Table 1. Chi^2 test of goodness of fit of observed frequencies to frequensies expected from the logarithmic series for benthic infauna from eight stations in Puget Sound.

Station	Date	Chi^2	Degrees of Freedom	p(0.05)
1	February 1963	37.8	5	11.07
1	April 1963	25.2	5	11.07
2	February 1963	2.8	3	7.81
2	May 1963	21.0	3	7.81
3	February 1963	3.7	6	12.59
3	April 1963	8.6	6	12.59
4	January 1963	25.7	5	11.07
4	April 1963	10.6	5	11.07
5	February 1963	11.5	5	11.07
5	April 1963	8.2	5	11.07
6	February 1963	8.6	5	11.07
6	April 1963	12.9	6	12.59
7	February 1963	2.2	3	7.81
7	April 1963	21.8	5	11.07
8	February 1963	9.8	5	11.07
8	April 1963	6.4	5	11.07

The discrepancy between the observed and the expected frequencies was particularly high at stations with a high degree of numerical dominance, and the deviation from the logarithmic series (D) for the first five classes (species with from one to five specimens) appeared to be positively correlated to the redundancy (R) (Fig. 2). The correlation is weak, probably largely because of sampling variability for the rare species, but KENDALL's rank correlation coefficient was 0.61 ($p < 0.01$). A test of the relationship between goodness of fit to the logarithmic series and redundancy could be performed if the redundancy could be manipulated and the subsequent change in the goodness of fit studied. Stations 1 and 3 were quite similar in species composition and about the same species were numerically dominant at the two stations (LIE 1968); however, station 1 had a very high and station 3 a very low redundancy. When the data from these two stations from February 1963 were pooled, the combined redundancy as expected became lower than at station 1 but higher than

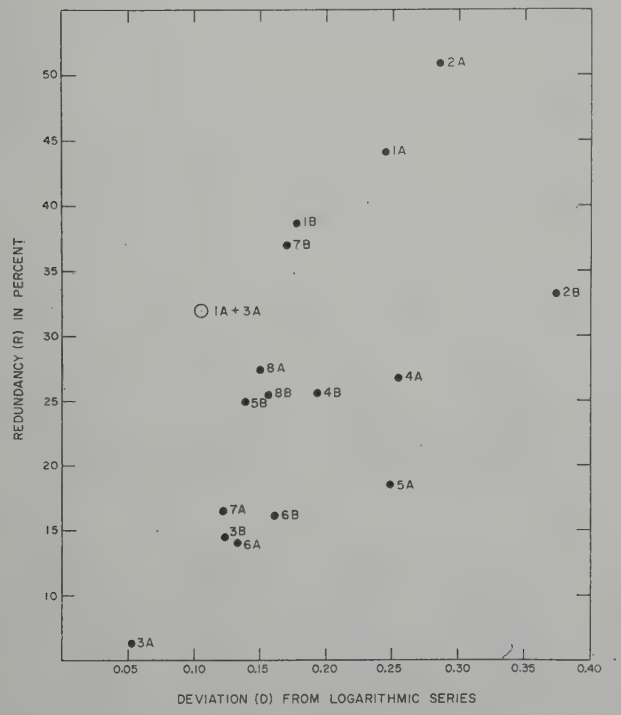

Fig. 2. The relationship between redundancy and the deviation of observed frequencies from frequencies expected from the logarithmic series at eight stations in January–February (A) and April–May (B) 1963.

at station 3. Consequently the deviation from the logarithmic series (Fig. 2) became lower than for station 1 but higher than for station 3.

Several examples of poor fit to the logarithmic series in collections of insects with strong numerical dominance by one or a few species are discussed by Williams (1964). A characteristic feature of these situations, as for the benthic infauna, was a too high number of species with only one specimen. In communities with strong dominance the basic assumption of a Gamma-distribution of the species abundances may not be satisfied.

One of the underlying assumptions for the logarithmic series is that the species are randomly and independently distributed. However, non-randomness of spatial distribution occurs frequently in nature (Hairston 1959) and Lie (1968) showed that most of the numerically dominant species at the stations in Puget Sound had varying degrees of patchiness. The measured patchiness is in part a function of sampling design and sampling techniques. Certain sampling techniques, such as using light traps to attract and capture insects (Williams 1964) and trawling for bottom fish (Taylor 1953), have provided data with particularly good fit to the logarithmic series. However, these sampling techniques tend to obscure real patchiness of the fauna and thus they induce randomness. In the benthic communities in Puget Sound a considerable portion of species are commensal (viz. members of the polychaete family Polynoidae and the crustacean family Pinnotheridae), and consequently the requirement of independence is often not satisfied.

Benthic communities, particularly in the arctic and boreal regions, are characterized by dominance in abundance or biomass by a small number of species (Thorson 1957) and normally there is patchiness and a considerable degree of interdependence among the species. As the basic assumptions for the logarithmic series are randomness of spatial distribution and independence among the species, and as the series appears to be adversely affected by numerical dominance, it is doubtful if the series generally is a representative model for the relationship among species and specimens in a benthic infaunal community.

THE LOGNORMAL DISTRIBUTION

The data from January–February and April–May 1963 were grouped in $\times 3$ classes (Williams 1953) and the cumulative percentages were plotted on logarithmic probability paper (Fig. 3). The curves are reasonably straight, which indicates that the distributions are close to the lognormal. However, all the curves are characterized by having the median (50% probability) in the first or second class, indicating that half or more of the species had not been sampled. By increasing the sample

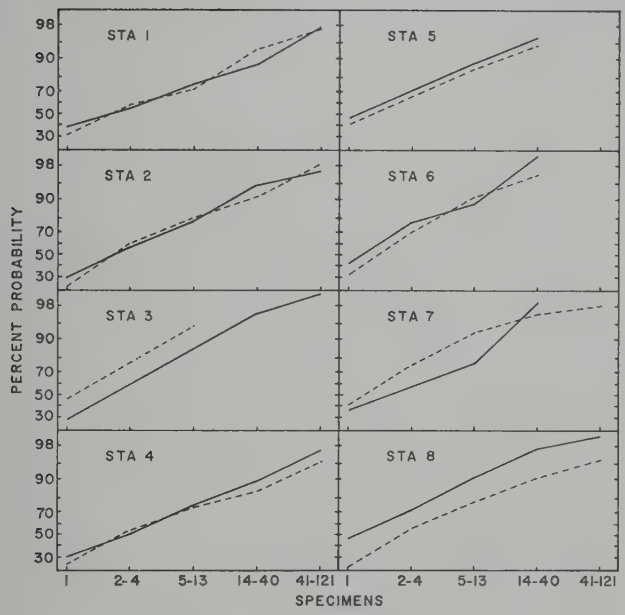

Fig. 3. Cumulative percentage distribution of species in $\times 3$ classes of abundance. Solid line; January—February 1963; broken line: April—May 1963.

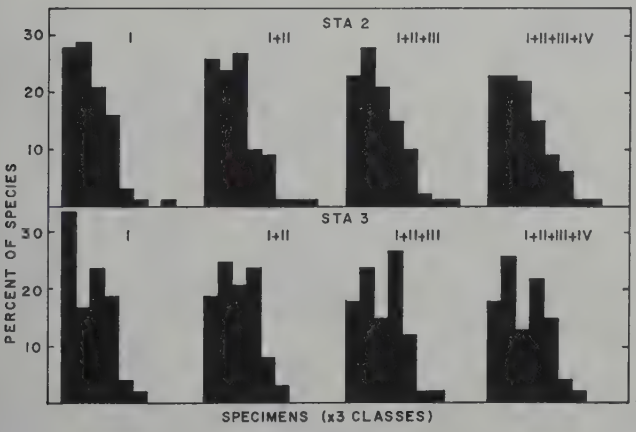

Fig. 4. Percentage frequency distribution of species in $\times 3$ classes of abundance at stations 2 and 3. Combined data from January–February (I), April–May (II), August (III), and November (IV) 1963.

size the median should shift to the right on the abscissa (Preston 1948), i.e., the first class should contain a progressively lower percentage of the total number of species. Williams (1953) showed that the mode of the lognormal distribution of insects caught in light traps shifted to the right when the sampling time was increased from an eighth of a year to eight years. The faunal assemblages in Puget Sound exhibited small variations in number of species and the numerically dominant species remained largely the same throughout the investigated period (Lie 1968). Combining the data from different cruises for a station would then, as for Williams' insect data, in effect be increasing the sample size. Fig. 4 shows the percentage frequencies of the total fauna at station 2 and the non-polychaetes at station 3 when data were combined for the four cruises in 1963. A significant shift of the mode can hardly be ascertained; even after combining all four cruises the curves are strongly truncated, although a reduction in the percentages of the first class did take place.

The constancy of total number of species during the investigated period does not necessarily imply that the same species always were present. Fifteen of the species (23%) found at station 2 in May were not found in February, eleven species (17%) found in August were not found during the two preceding cruises, and nine species (12%) found in November were not found during the three preceding cruises. Similarly, twenty-five of the species (45%) found at station 3 in April were not found in February, eleven species (19%) found in August were not found during the two preceding cruises, and seven species (12%) were not found during the three preceding cruises. Therefore, by increasing the sample size it appears that the chance of encountering new species was nearly as high as the chance of adding new specimens to earlier recorded rare species. Hairston and Byers (1954) did not find a significant shift of the mode of the lognormal distribution with increasing sample size, and they argued that the reason for this was the extreme patchiness of the rare species.

When communities are considered more or less well defined stages in a "continuum" (Whittaker 1967), a certain number of the rare species will be representatives of neighbouring communities. Increasing the sample size will lead to discovery of more of these rare, transient species, and the lognormal distribution will always be strongly truncated. An upper limit of the number of species in a community cannot be defined (Brian 1953), except the limit set by the respective zoogeographical regime. Lie (1968) found a gradual transition in faunal composition among the eight Puget Sound stations. The benthic communities appear to be arrayed in a continuum that is directly related to physical properties of the substrate. When the data from all seven seasons were

combined for each station and for all the stations, thus effectively increasing sample size, the lognormal distributions were still strongly truncated for the individual stations (Fig. 5). In contrast, the distribution for the combined data was considerably less truncated. Therefore, it appears that the sampling at the eight stations in Puget Sound during 1963–64 was sufficient to encompass the majority of the species in this relatively well defined geographical area.

Complete or nearly complete lognormal distributions have been demonstrated in large samples from well defined geographical areas such as islands (Preston 1962) and in samples covering a very large area or collected over a very long time (Williams 1964). Such samples will contain species from more than one community, and the lognormal distribution is therefore a model for the "between habitat" species diversity (MacArthur 1965).

Benthic communities may be identified as "statistical units" based on the presence of characteristic species (Thorson 1957) or ordinated in multi-dimensional space by multivariate analysis (Cassie and Michael 1968), but regardless of technique of analysis the communities must be considered "open" in the sense that there are no distinct borders between them. The lognormal distribution in such communities will be strongly truncated and therefore not be a better model for the distribution of specimens among the species than the logarithmic series.

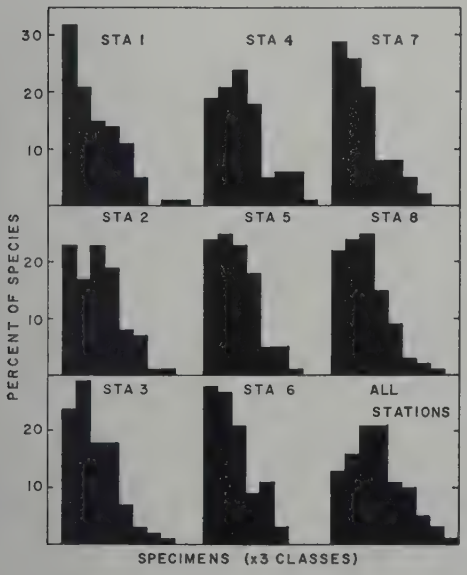

Fig. 5. Percentage frequency distribution of species in $\times 3$ classes of abundance. Combined data from 1963–1964 for single stations and for all stations.

SUMMARY

1. Benthic infauna collected at eight stations in Puget Sound during 1963–1964 was tested for agreement with the logarithmic series and the lognormal distribution.
2. The data agreed only moderately well with the logarithmic series; seven of sixteen cases showed statistically significant differences between observed frequencies and frequencies expected from the logarithmic series. Furthermore, there was an inverse relationship between goodness of fit to the logarithmic series and the level of numerical dominance of the faunal assemblages. This relationship, and the fact that the underlying assumptions for the logarithmic series are not applicable in benthic communities, makes the series a doubtful model for the relationship between species and specimens in a benthic community.
3. The lognormal distribution fitted the data reasonably well, but the curves were always strongly truncated. Increasing the sample size reduced the percentage of species in the first class somewhat, but only when the data from all the seasons and all the stations were combined was a significant part of the distribution "unveiled". The lognormal distribution therefore represents the geographical region reasonably well, but for each station the curves are too truncated to represent better models than the logarithmic series.

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FEEDING RATES OF CETACEA

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INTRODUCTION

A variety of porpoises and dolphins of the superfamily Delphinoidea, ranging through three magnitudes of weight from the harbour porpoise *Phocoena* to the killer whale *Orcinus*, have now been kept in captivity. From aquarium records of body weights and weights of food ingested, daily food consumption can be determined. Following Ivlev (1961) I shall call this index the daily ration. There is no suitable term in the literature for the index daily ration expressed as percent of body weight which I shall therefore call the feeding rate. The purpose of this paper is to attempt to discover the feeding rates of whales which are too large to have yet been kept in oceanaria.

MATERIAL AND METHODS

Table 1 summarises the results of a literature search on feeding rates, supplemented by unpublished information obtained by correspondence with curators of various oceanaria. Least information was obtained for body weight, since curators are loath to weigh living animals, especially those of large size, and estimates of weight are usually too inaccurate to be useful. An independent search of literature and unpublished records on length and weights of whales, however, allowed construction of curves from which weight could be determined knowing body length; this information was useful for the killer whale *Orcinus*, for example. Data on body weight and daily ration, from which feeding rate could be calculated, were found for 8 genera of Delphinoidea maintained in captivity, ranging through 2 orders of magnitude of body size. Details are as follows:

Contribution given in honour of Gunnar Rollefsen at his 70th birthday.

Table 1. Summarised data on feeding rates of Delphinoidea in captivity.

Species	Number of animals	Location	Mean body length m	Mean body weight kg	Mean food weight per diem kg	Food as percent body weight	Number of daily feeds
Phocoena phocoena	8	Strib, Denmark	1	40	4.3	10.8	3–4
Lagenorhynchus obliquidens	2	Vancouver, British Columbia	2	87	6.8	7.9	?
Phocoenoides dalli	1	Pt. Mugu, California	2	120	15	11.3	5
Tursiops truncatus	2	Pt. Mugu, California; Montreal, Quebec	2	168	7.0	4.2	2
Globicephala macrorhyncha juv.	1	Marineland, Florida	1	ca190	24.1	12.7	?
Delphinapterus leucas	2	Vancouver	2.8	238	23	5.5	2
Delphinapterus leucas	4	New York City	3.4	468	23	5.1	?
Pseudorca crassidens	1	Marineland of the Pacific, California	3.6	437	20.9	4.7	?
Globicephala scammoni	3	Marineland	5	842	33.2	4.0	?
Orcinus orca	4	Vancouver. Sea World, Calif.	4.75	1258	51	4.05	?

(Data on animals or groups of animals used in calculating feeding rates in Table 1 are shown by an asterisk in the text.)

Phocoena phocoena.

Harbour porpoise. ANDERSEN (1965, Tables 1 and 2) gave weights and daily rations of 7 porpoises held in captivity at Strib, Denmark. All but two of the animals were weighed at death, the other two at a point midway through experiments. Most of the animals presumably increased in weight during this period. The food was fish: herring, *Clupea harengus* and whiting, *Gadus merlangus*. From ANDERSEN's data I calculate that the mean weight at death was 51 kg, and the mean ration was 4.3 kg per diem. Hence the minimum estimate of feeding rate is 8.26%. ANDERSEN gives the mean body weight during captivity as

40 kg and the mean feeding rate about 10% (accurately 10.8%).* I have used this figure in calculating the feeding rate in Table 1, but necessarily weight at death in calculating its variability between animals in Table 2.

Table 2. Feeding rates of individual *Phocoena* (data from ANDERSEN 1965; Tables 1 and 2).

Animal number	Season (summer, winter)	Duration (months)	Food per diem (kg)	Animal weight (kg)	Feeding rate (Weight of food × 100 / Weight of animal)
1	W	5	3.0	—	—
2	S	1	2.0	38	5.26
3	S	2	4.1	32	12.81
4	W	3	5.4	63	8.57
5	W	3	4.8	55	8.73
6	S	2	4.1	30	13.67
7	W	5	4.1	68	6.03
7	S	5	4.8 (4.5)		7.06
8	S	5	4.2	71	5.92
8	W	5	5.1 (4.6)		7.18
Mean of animals 2 to 8			4.2	51	8.26
Range			2.0–5.4	32–71	5.26–13.67

Lagenorhynchus obliquidens.

Pacific white-sided porpoise. ANON (1968 a) gave the length of a male as 6 ft (183 cm) and weight 198 lb (90 kg); the weight of a companion female 185 lb (84 kg). Their food consumption was 15 lb (7 kg) of herring, *Clupea pallasii* and mackerel, *Pneumatophorus diego*, per diem (ANON. 1967 a).*

Phocoenoides dalli.

Dall porpoise. RIDGWAY (1966) gave the daily feeding rate of a specimen of weight 120 kg as 15 kg of mackerel, *Pneumatophorus diego*, in 4 feeds per diem.*

Tursiops truncatus.

Bottlenose porpoise. RIDGWAY (personal communication), gave the feeding rate of a female *T. truncatus* of weight 390 lb (177 kg) as 16 lb (7.3 kg) per diem of mixed fresh mackerel, *Pneumatophorus* and smelt, *Osmerus mordax*. Mr. BRIAN BECK (personal communication) from experience at the Montreal Aquarium gave the feeding rate of a female *T. truncatus* of weight 350 lb (159 kg), fed on herring and smelt, as 30 lb

(13.6 kg). However at this rate of feeding, the animal soon reached satiety and ceased to feed. With a free choice, the average daily intake levelled off to 15 lb (6.8 kg) per diem after 11 days. Feeding rate for both experiments agrees at 4.2% (Table 1).*

Delphinapterus leucas.

White whale. Anon. (1968 a) gave the current lengths of two white whales as 10.5 and 8 ft (320 cm, 244 cm) and the lengths at capture, on September 16 1967, as 10 ft 4 in and 7 ft 5 in (315 cm, 226 cm). Anon. (1967 b) gave the weight of the calf as 490 lb (223 kg) having increased from 238 lb (108 kg) at capture. Anon. (1967 a) gave the feeding rates as 50 lb (23 kg) of herring and salmon (*Onchorhynchus* sp.) for the adult and 25 lb (11.5 kg) for the young animal, but the calf was reported to be taking some food from the adult. I calculate the adult's weight to have been 300 kg, the weight of the young animal in November–December 165 kg, giving estimated feeding rates of 4.1 and 6.9%.*

Mr. R. Morris (personal communication) gave me details of two male and two female white whales held at the New York Aquarium. Lengths ranged from 10 to 13 ft with a mean of 11 ft 3 in (3.43 m). Weights were estimated at from 700 to 2000 lb with an average of 1250 lb (567 kg), and feeding rates from 40 to 60 lb per animal per diem with an average of 50 lb (23 kg) in two daily feeds, giving an estimate of feeding rate of 4.1%. These weights however, were estimates and may have been high. Known weights of the four animals were given to me by Morris and Mr. P. Montreuil as: two females at capture in August 1967—625 lb (284 kg) each; the larger male, on May 17, 1965—1181 lb (538 kg). Dr. J. R. Geraci (personal communication) estimated the weight of the two males in 1967 at 900 and 1100 lb. All these weights had presumably increased by February 1968 when the feeding rate was given by Morris. Using the known weights one obtains a mean weight of 369 kg and a mean feeding rate of 6.2%. The mean of the two estimates of feeding rate for the New York animals is 5.1%.*

Pseudorca crassidens.

False killer whale. Brown, Caldwell and Caldwell (1966) gave the cumulative food consumption of a captive female false killer whale between November 4, 1963 and August 31, 1965 as 30,650 lb (13,903 kg) of fish and squid. I calculate a mean daily ration of 45.95 lb (20.84 kg). The animal weighed 825 lb at capture and 1100 lb at writing. Taking the mean weight at 962.5 lb (456.6 kg) I find a mean daily feeding rate of 4.7% of body weight.*

Globicephala macrorhyncha.

Southern Atlantic pilot whale. KRITZLER (1952) gave a total food consumption of a young captive pilot whale at Marineland, Florida, between October 6, 1948 and July 5, 1949 as about 7 tons of squid, plus small, unmeasured quantities of fish. Weight at capture was estimated at 300 lb and at death 505 lb. Daily food consumption was at least 53.03 lb (squid only) and mean weight during this period at least 400 lb, giving a daily feeding rate of 4.7% of body weight.*

Globicephala scammoni.

Pacific pilot whale. BROWN (1960, 1962) and GILMORE (1962) gave the weights and daily feeding rates of three Pacific pilot whales held at Marineland of the Pacific, California, in about September, 1959: the smallest weighed an estimated 1100 lb and ate 40–45 lb of food daily; the median animal weighed 1360 lb and ate 80 lb daily; the largest weighed an estimated 3000 lb and ate 100 lb of food daily. For the median animal, of known weight, the feeding rate was 5.9% of body weight per day. Taking the mean of the three weights, known and estimated, as 1850 lb, and the mean daily ration as 74 lb, the mean feeding rate is calculated at close to 4.0% of body weight per diem.*

Orcinus orca.

Killer whale. A female at the Vancouver Aquarium on January 16, 1968 measured 16 ft 2 in (4.9 m) along the curve of the back, or 15 ft 6 in (4.7 m) in a straight line (ANON. 1968 a). In November, 1967 this animal ate 110 lb (50 kg) of herring and ling cod, *Ophiodon elongatus*, daily (ANON. 1967 a). The weight of this animal was estimated at 2500 lb (1136 kg), giving an estimated feeding rate of 4.4% per diem.* A previously-captured male, length 15 ft 4 in (4.67 m), weighed 2300 lb (1040 kg) and ate a steady diet of 100 lb (45 kg) daily (NEWMAN and MCGEER 1966), giving a feeding rate of 4.3% of body weight per day.* A male killer whale of length 16 ft (49 m) held at Pender Harbour, British Columbia, ate 130 lb (59 kg) of herring daily before its escape (ANON. 1968 b). From a weight/length curve I calculate its weight to have been about 1500 kg, giving a feeding rate of 3.9%.* [Data for construction of the weight/length curve for *Orcinus orca* were obtained from the compendium of SCHEFFER (MS 1967), from SLEPTSOV (1961) and BURGESS (1968)]. BURGESS (1968) gave the daily food intake of a killer whale at Sea World, San Diego California, as between 36 and 63 kg, or a mean of 49.5 kg. The length at capture in October, 1965 was 4.1 m and the

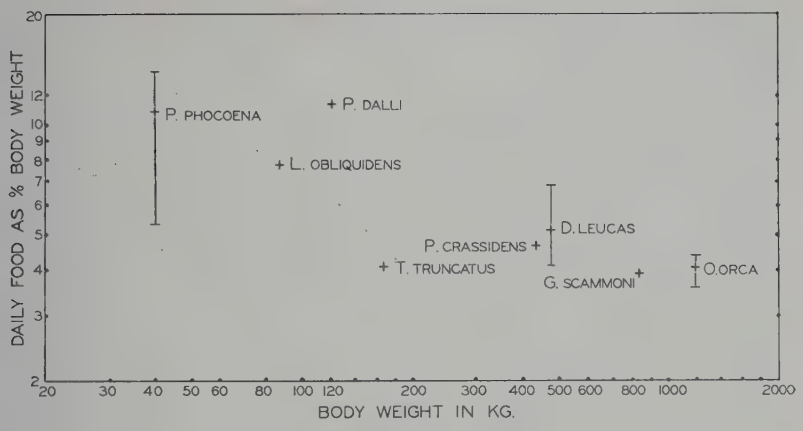

Fig. 1. Feeding rates of Delphinoidea.

weight 1088 kg. The length after 17 months was 4.5 m and the weight had increased about 270 kg, implying a weight at writing of about 138 kg. I calculate a daily feeding rate of 3.6% of body weight daily.*

RESULTS

Fig. 1 shows that the feeding rate decreases from the smaller genera of Delphinoidea to the larger, but levels off at about 4 to 5% of body weight for genera of length 2 m (weight 650 kg—adult *Tursiops*) or greater.

This pattern is complicated by several factors:

(*a*) Differences occur in feeding rates between young and adult animals.

Best data are those of Andersen (1965) for *Phocoena* which show a variation in feeding rate of from 5.26 to 13.67% for 7 animals (Table 2). With the exception of one short-lived and probably sick animal (No. 2), which was small yet fed at a low level, feeding rate was inversely proportional to body weight. Only two animals, having weights of less than 30 kg, showed feeding rates in excess of 10% of body weight. Møhl-Hansen (1954) gave birth weight of Danish porpoises as 6–8 kg, weight at full weaning as 25 kg, so that the animals below 30 kg in weight were young.

A young pilot whale, *Globicephala macrorhyncha*, showed a feeding rate of 13% (Kritzler 1952). This is twice as high as the feeding rate of an adult *G. scammoni*, which was 6% of body weight (Table 1).

The young *Delphinapterus leucas* held in captivity consumed about 6.9% of body weight per diem compared to its mother's consumption of about 4.1%. However the account makes clear that the young animal

stole food given to the mother, which would increase further the disparity between the feeding rates.

(*b*) Species differences occur between genera of the same weight.

Phocoenoides dalli has a higher feeding rate than the slightly smaller *Lagenorhynchus obliquidens*, as well as the larger *Tursiops truncatus*. *Phocoenoides dalli* is exceptional also in having a high metabolic rate, large heart, thin fat layer and ability to dive very deep (Ridgway 1966). Ridgway and Johnston (1966) gave the heart weights of these three species, which I have included in Table 3. Heart weights are exactly proportional to daily feeding rates, being close to 0.11 × feeding rate, as follows:

Species	Body weight kg	Feeding rate %	Heart weight	Heart weight / Feeding rate
L. obliquidens	87	7.8	8.5	0.109
P. dalli	120	11.3	13.1	0.116
T. truncatus	168	4.2	5.0	0.119

This result is not unexpected since both heart weight and feeding rate are expressions of metabolic rate. *P. dalli* appears to be exceptional also in the number of daily feeds necessary in captivity to maintain its high metabolism; 5 compared with 2 for *Tursiops truncatus* and *Delphinapterus leucas*; 3 or 4 for *Phocoena phocoena*. While the metabolic rate of many genera is not known, we now have three measures of it: proportional heart weight, feeding rate, and number of daily feeds.

DISCUSSION

The measures of the metabolic rate give us a key to discovering the feeding rate of large whales which cannot yet be kept in captivity. The assumption involved is that heart weight retains the same proportionality to feeding rate in large whales as in the Delphinoidea. I made a literature search on total weights and heart weights of whales starting from the paper of Slijper (1958). The main references were: Bjarnason and Lingaas (1954); Fujino (1955); Kleinenberg (1956); Kleinenberg *et al.* (1964); Laurie (1933); Nishiwaki (1950); Ohno and Fujino (1952); Omura (1950, 1957); Quiring (1943); Ridgway and Johnston (1966); Sleptsov (1961); Slijper (1958); and Tomilin (1967), the last quoting several Soviet authors. Results are summarised in Table 3 and Fig. 2.

Adults of the large whalebone whales (Mysticeti) are seen to have heart weights of 3.5 to 6‰ of body weight. For good numbers of 4 species

Table 3. Body and heart weights of Cetacea.

Species in order of increasing size	No. of specimens	Body length cm	Mean body weight kg	Heart weight × 1000 Body weight	
				Range	Mean
Phocoena phocoena	27	67–171	35.9	6.5–12.2	8.4
Delphinus delphis	50	—	54.2	—	4.84
Phocoenoides dalli	3	—	97	12.5–13.4	13.1
Lagenorhynchus obliquidens	5	—	110	7.0– 9.2	8.5
Tursiops truncatus	50	—	133	—	5.00
Kogia breviceps	1	298	417	—	3.26
Delphinapterus leucas	20	327–425	821	3.7– 6.9	5.7
Globicephala melaena	1	—	1,230	—	4.4
Orcinus orca	3	495–650	2,288	5.0– 7.3	6.41
Balaenoptera acutorostrata	1	790	4,846	—	4.75
Berardius bairdi	1	—	8,560	—	6.30
Balaenoptera borealis	17	1160–1460	12,551	3.4– 4.9	4.04
B. brydei	20	1220–1380	13,077	2.3– 6.8	4.6
Eubalaena glacialis	2	1160–1250	22,556	6.9– 7.9	7.4
Eschrichtius glaucus	1	1335	31,466	—	5.47
Megaptera novaeangliae	4	1250–1390	31,913	3.6– 5.8	5.31
Physeter macrocephalus	30	1110–1800	31,525	2.4– 6.1	3.32
Balaenoptera physalus	29	1860–2320	51,632	2.3–11.0	3.96
B. musculus	32	2130–2710	85,520	3.7– 6.7	3.99

of rorqual (*Balaenoptera borealis*, *brydei*, *musculus* and *physalus*) the mean figure was close to 4‰; for smaller numbers of humpback, *Megaptera novaeangliae* and right whales, *Eubalaena glacialis*, the figure was about 5 to 6‰. It was significantly lower at 3.4‰ in a good series of sperm whales, *Physeter catodon* and, perhaps also significantly, in one specimen of the related pigmy sperm whale, *Kogia breviceps*. Data were scarce for medium-sized whales: a single specimen of lesser rorqual, *Balaenoptera acutorostrata*, gave 4.8‰ and SLIJPER without stating details of size gave a figure of 5.1‰ for a second specimen of this species. A heart weight/body weight ratio of 6.3‰ for one specimen of *Berardius bairdii* is too little to provide a reliable figure for the Ziphiidae. I have been able to find less data for the Delphinoidea than for large whales. Three adult specimens of adult killer whales, *Orcinus orca*, gave a proportional heart weight of 6.35‰; 20 white whales, *Delphinapterus leucas*, 5.7‰; 50 *Tursiops truncatus* 5.1‰; 50 *Delphinus delphis* 4.8‰; and 27 *Phocoena phocoena* 8.4‰. The data do not disagree with the previous conclusion that the heart weight/body weight ratio is equal to about one tenth of the feeding rate.

Heart weight is higher for young than for adult Cetacea of the same species. For *Delphinus delphis*, KLEINENBERG (1956) gave heart/body weight

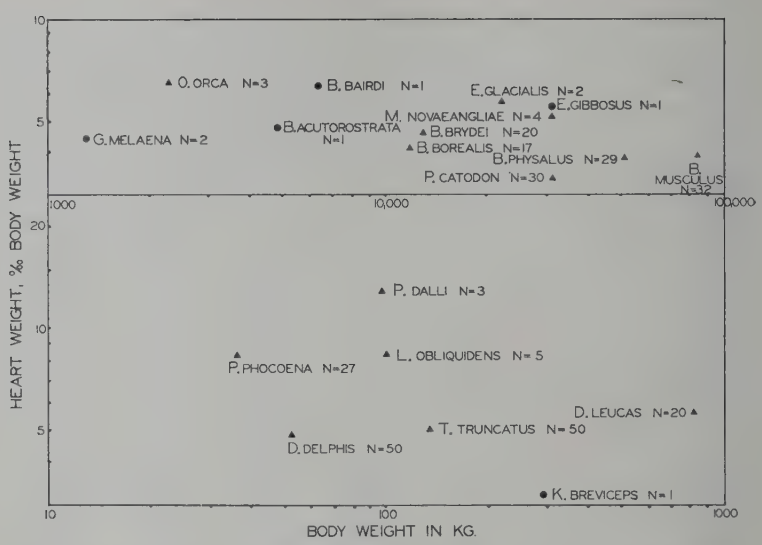

Fig. 2. Heart weight/body weight ratios of Cetacea. Solid circle—single animal; triangle—mean of more than one animal. N = number of animals from which data obtained.

ratios of 7.59‰ for late embryos, 6.93‰ for underyearlings and 4.84‰ for older animals. The data of Slijper (1958) suggest the same for *Tursiops truncatus*: 9.4‰ for a juvenile compared with 5.0‰ for Kleinenberg's adult sample; and also for *Lagenorhynchus acutus*: 17.7‰ for a newborn animal compared with 8.5‰ for Ridgway and Johnston's (1966) adult sample of the related *L. obliquidens*. However Slijper's (1958) data for 27 *Phocoena phocoena* show no decline in heart weight/body weight ratio with increase in body weight (age). This exception suggests that *Phocoena* (like *Phocoenoides dalli*) may retain a high metabolic rate throughout life. However, Kleinenberg's data for Black Sea *Phocoena phocoena* gave a mean heart weight/body weight ratio of only 4.5‰ for 50 Black Sea *Phocoena*, indicating that the question must be re-examined.

Assuming that the ratio of heart weight to body weight equals approximately one tenth of the feeding rate in large whales, I conclude that the large rorquals eat some 4% of their body weight daily. A lower figure for *Physeter* seems quite reasonable since *Physeter* feeds through the eyar, but the large rorquals feed during the summer months only.

Klumov (1963) has deduced from data on maximal stomach con-

Table 4. Weights of full stomachs of some Mysticete whales.

Species	Region	Length (m)	Body weight (metric tons)	Weight of stomach contents (metric tons)	Ratio
Blue	Antarctic	24	65	1.10 *a*)	1.7
Fin	N. Pacific	22	57*f*	0.85 *b*)	1.5
Fin	N. Pacific	18.5	35	0.75 *c*)	2.0
Fin	N. Pacific	18.5	35	0.76 *d*)	2.2
Sei	N. Pacific	12	10*e*	0.60 *d*)	2.0

a) KLUMOV 1963 p. 141, *b*) KLUMOV 1963 p. 149, *c*) KLUMOV 1963 p. 154, *d*) NEMOTE 1959 pp. 218–220, *e*) OMURA 1950, *f*) NISHIWAKI 1950.

tents of Mysticeti and the biomass of planktonic food that " the whalebone whales require about 30–40 g per kg of live weight daily." This conclusion agrees well with my own. " Proceeding from the above indices " says KLUMOV " the 24-hour long requirement of food for the blue whale of average size and weight (23.5–24.5 m, 60–70 tons) is 2–2.5 tons." KLUMOV makes clear that this level of feeding is optimal, depending on an adequate biomass of plankton or pelagic fish. Table 4 shows data on maximum stomach volumes of large rorquals. With KLUMOV's suggested feeding rate, the ratio of stomach volume to body weight suggests a twice-daily feeding rate for blue, fin and sei whales. By contrast IVASHIN (1961) suggests that the daily food consumption of a humpback whale, *Megaptera novaeangliae*, in Antarctic seas in February is about 4 metric tons, with feeds every 3–4 hours. Assuming a body weight of about 25 tons the feeding rate would be 16%, which would demand a much higher metabolism of *Megatera* than of the genus *Balaenoptera*. Such a feeding rate would be comparable with that of *Phocoenoides dalli* among the Delphinoidea and would necessitate a large heart. The average heart weight for 4 large specimens of *Megaptera* is 5.3‰, which is higher than for the species of *Balaenoptera*, but not as high as IVASHIN's suggestion would require. I conclude that KLUMOV's assumptions on feeding rates are probably closer to reality than IVASHIN's.

The data of KLUMOV (1963) and NEMOTO (1959) on stomach contents suggest that baleen whales rarely find optimal quantities of food, at least in the North Atlantic and Pacific Oceans; this would imply that they must actively search out feeding concentrations. The sensory and navigational basis of this search has yet to be discovered.

SUMMARY

1. The feeding rate of a whale is defined as the weight of daily food ingested expressed as percentage of body weight. Records of daily rations of Delphinoidea (porpoises and dolphins) in captivity allow calculation of feeding rates for eight genera having adult body weights of 10^1 to 10^3 kg.

2. There is an inverse relation between feeding rate and body weight, both between species and between young and adult Delphinoidea. The range of feeding rates is from 12–13% to 4–6%. Above a body weight of 6×10^2 kg, represented by adult *Tursiops truncatus*, feeding rate remains constant at 4–6% up to the largest species in which it has been measured, the killer whale, *Orcinus*, of body weight 2×10^3 kg.

3. Heart weight expressed as proportion of body weight varies directly with feeding rate and is equal to about one tenth of it. Young animals of all species, as well as adults of *Phocoenoides dalli* and possibly *Phocoena phocoena* have high feeding rates and heart weights, showing that both indices measure metabolic rate. From their heart weight/body weight ratio an attempt has been made to calculate feeding rates of whales too large to be kept in aquaria.

4. Heart weight/body weight ratios of adults rorquals of the genus *Balaenoptera* are about 4‰; of sperm whales, *Physeter* and one example of the small, related *Kogia*, lowest of all at 3.5‰. These data suggest a feeding rate of 4% for adult rorquals, so that from curves relating body length and body weight, their daily food consumption may be calculated.

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My debt to a number of skilled curators of aquaria is, I hope, adequately expressed by mention of their names in the text. Dr. E. D. Mitchell gave valuable stimulus and criticism in the development of the paper.

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INTRASPECIFIC STRUCTURE AND VARIABILITY IN RELATION TO FISHERIES MANAGEMENT

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INTRODUCTION

Cod is nothing but cod, a fish species, *Gadus morhua* L. This species is caught nowadays with trawls in the north Atlantic and on the Newfoundland banks, in the Barents Sea as well as in the northern Pacific, near the coasts of northern Asia and northern America. This fish is also caught with long lines and hooks in the Norwegian fjords and the White Sea and is known to have been fished by pomors in the last century and by middle age vikings. Cod was fished by the stone age man who populated the Norwegian coast, the Russian Murman and the Pacific coastal areas thousands of years ago.

It is yet uncertain when cod originated as a species, but as far as a number of other species of the same boreal faunistic complex, mostly fresh water fishes, are concerned, they are known to have originated in the mid tertiary period. Most zoologists nowadays regard species as an objective reality, as a form of existence of the living matter. Animal species is not a conventional concept, it is not "what a good taxonomist considers a species", but an actually existing multitude of specimens which possess some specific-qualitative properties characteristic for the given species and relatively stable in time and space. It means that a species which once originated exists a more or less long period of time (so far as the specific environment exists) retaining its specific properties.

As regards freshwater fishes, perch, pike, pike-perch, catfish and some others, they are known to have undoubtedly existed since pliocene time and possibly earlier. At approximately the same time most species representative of the boreal sea fauna complex, cod, oceanic herring, plaice and flounders, etc. were formed (Nikolsky 1968). However, the

Contribution given in honour of Gunnar Rollefsen at his 70th birthday.

stability of the species over thousands, and possibly, millions of years is ensured by the intraspecific variability, by its elasticity, so to say.

Stenobiotic species adapted to live under relatively stable, abiotic and biotic life conditions reveal a lower variability, lower elasticity. Usually, their intraspecific structure is simpler. An example of this type of stenobiotic fishes with a very low variability could be supplied by most of the species populating coral reefs, e.g. Pomacentridae. These species are extremely low-variable, occupying as a rule, a very limited distribution area and being adapted to very stable life conditions. They perish when these conditions change beyond the limit of this fish's very low specific adaptability.

Eurybiotic species, such as Arctic chars and cod, possess a much wider range of adaptability, a considerable intraspecific variability and a more complex intraspecific structure. Thus, every species represents an open self-regulating system in a permanent interaction with the environment which incessantly keeps adapting to the changing conditions. This system possesses at the same time certain morphological, physiological and ecological characters distinctive for the species as a system.

INTRASPECIFIC VARIABILITY

For fishery biologists, endeavouring to develop a scientific basis for fish resource exploitation, the knowledge of the elasticity and the structure of the given species-system of economic importance is quite essential. Principal mechanisms operating in the populations provide changes in number and biomass due to respective environmental changes, first and foremost in the food supply rate which is manifested in growth changes. As is known, the increase in growth rate is related to a faster achievement of maturation age and an increase in fecundity. A faster growth is related to reduction of mortality rate, for, as a rule, bigger fish fall prey to predators on a larger scale than the smaller ones. Principle mechanisms of population self-regulation in connection with food supply changes have been rather well studied (Nikolsky 1950, 1962 and 1969, Rollefsen 1954, Schaefer 1956 and others) and a detailed account is uncalled for here.

However, the process in question is often found not to be as direct as in the above scheme, being considerably affected by a number of factors, and, in particular, by mutual interactions of fish in different number of year-classes. A numerous year-class may handicap the growth rate of both preceding and following generations. The problem calls for further investigation for it is of a great theoretical and practical interest, first and foremost, in forecasting of the mature stock recruitment. A review of the data on the problem was reported by Polyakov (1962).

Changes in spawning periodicity appear to be an essential form of self-regulation. In fact, in years when the stock of White Sea herring is numerous a part of the females may leave out a spawning period. Due to food supply insufficiency they fail to fatten during a single feeding period (Cheprakova 1966). This phenomenon is also observed in some freshwater species, e.g. in whitefish (Reshetnikov 1967). It should be noted that many species inhabiting the northern part of the distribution area reproduce every other year, southern populations reproducing annually. Besides whitefish, this has been found in bream and some other species (Koshelev 1966). It is interesting that in some species in the southern part of the distribution area, e.g. in bream, portioning in spawning is observed, i.e. the reproduction rate speeds up.

An essential, though yet poorly investigated, mechanism of self-regulation is change in the variability of specimens in the population. Food supply increase is, as a rule, related to a reduction in the year-class size variability. This has been most clearly demonstrated in Baltic herring larvae (Anokhina 1969). Strong year-classes are distinguished by a wider variability range that weaken year-classes. The food supply is determined not only by the numbers of fish in an age group, but by the development of its food resources, and equally important, the coincidence of the food plankton period with fry development. This regularity, though manifested in a more complicated way, is noted for cod fry (Nikolsky, Belyanina, Ponomarenko and Sysoeva 1968). In the case of cod fry, the variability of characters is largely dependent on the size of the concentrations formed due to the dispersal over one or the other branch of the Atlantic current. Besides, in recent years, due to a low level of reproduction no feedback between the total number of cod fry and the food supply has been observed. This relationship was, however, revealed in specifically rich generation years, e.g. 1963.

The relationship between character variability and the quantity of cod fry is better demonstrated in coastal forms. In such stocks, as a rule, numerous populations prove to be most variable. An increase in variability makes it possible for the population to cope with more diversified environmental conditions. It has been most explicitly demonstrated for characters related to feeding and diet diversity. It is noteworthy, as was revealed in Murman coastal cod, that the diversity of characters in it slightly reduces with age in connection with a higher food supply level in fish at the age 1+ and 2+ as compared with specimens at the age of 0+.

One of the most essential specific characters which secure the existence of a species as a relatively stable unit, is the intraspecific structure. To a certain extent, all the intraspecific forms can be subdivided into four groups.

1. Geographical forms or subspecies, e.g. Atlantic cod and Pacific cod. The formation of subspecies enables the species to fill in a greater distribution area.

2. Ecological forms or infraspecies, e.g. fjord and migratory cod forms. The existence of various ecological forms enables filling in diversified habitats within the distribution area.

3. Seasonal forms, e.g. spring and autumn forms in salmon, autumn and spring spawning herring forms. This means of variability ensures filling in the same biotope to a greater extent in different seasons of the year.

4. Temporary forms, the forms which originate in the same biotope under changed life conditions in a population of any species. Such temporary forms are most markedly observed in numerous freshwater species, e.g. roach in the course of transition to the life in a reservoir newly formed at the river. In mammals such temporary subspecies are found in some fossil forms from the quarternary period, e.g. in Baltic region elk. The adaptive value of temporary subspecies lies in the capability of filling in the same biotope under changed conditions.

The diversity of the four intraspecific forms may be quite different ranging from a clear cut distinguishability to a gradual transition of one form to the other, clinal variability being in evidence. It should be mentioned in this connection that I do not find justifiable the fact that in the latest edition of the zoological nomenclature code taxonomic values are solely attributed to geographical categories, subspecies, the remaining intraspecific forms, being left out. Ecological and seasonal forms, however, often prove to be distinguishable to a greater extent than subspecies.

In many cases the appearance of ecological and seasonal forms is of a parallel character. The phenomenon faced is reminiscent of Vavilov's law of homologous rows (Nikolsky 1969). Possibly, as was suggested by Berg (1948) it is expedient to attribute the same specimens to such similar forms in different species, e.g. deep-water forms, infraspecies profundicola, lacustrine forms, infraspecies lacustris, etc. I believe that this scheme should be employed in zoological nomenclature code, subspecific individual names being retained.

IMPORTANCE FOR FISHERIES MANAGEMENT

For fishery biologists, the existence of intraspecific group forms within a species is extremely essential. When exploiting a certain population, dynamics of its number and distribution area should be taken into consideration. For example, the Arcto-Norwegian cod stock, being a unified self-recruiting form distributed over a great area, calls for a definite

exploitation scheme. If, as in the case of the northwestern Atlantic cod, some local forms are found, rational fishery should be arranged on a different basis than in the case of the Arcto-Norwegian stock. It is interesting to note that morphological indices in different age groups of the same form do not differ greatly in local forms of western Atlantic cod. In the Arctic cod, however, the distinctions in the morphology of different age groups within a form may be quite pronounced. This appears to be accounted for by highly variable life conditions in different age groups (Popova 1968). In numerous species there occur both large migratory forms and small coastal ones distinguished by a slower growth as well as an earlier maturation onset. The degree of isolation in these forms may range widely in some cases as in north Caspian roach. A coastal, smaller form may result from reproduction by a semi-migratory fast-growing one, and, evidently, vice versa. In other cases these forms may be isolated, one not reproducing the other.

In red salmon, *Oncorhynchus nerka* (Walb.), the migratory form reproduces in lakes a land-locked form, the so-called residual. In turn from this land-locked form a migratory form can be reproduced under certain conditions (Krokhin 1967).

It should be noted that in the course of the dwarf red salmon development some caryotypic changes occur, a great number of polyploid specimens appearing. This is of particular interest if polyploidy is related to an increased morphological variability. It is noteworthy that in migratory red salmon the caryotype is peculiarly stable (Chernenko 1968). The relationships between seasonal forms prove to be likewise diversified. If, e.g. in autumn- and spring spawning Baltic herring, a partial transition of one form to the other is evidently possible, in chum salmon this appears to be out of the question. It is natural that a fishery biologist aims at elucidating the relationships between the intraspecific forms, in particular, the possibility and conditions under which specimens of one form appear from the specimens of another form, i.e. whether one form can be reproduced by another and to what extent.

Thus, investigation of the theoretical aspects of the problem of species, further elucidation of the concept of species as a self-regulating system appears to be extremely essential for the solution of a number of fishery problems, and, first and foremost, for developing the basis of a rational exploitation of commercial species.*

* Dr. Rollefsen's paper on cod and cod fishery which he kindly sent me bears the following dedication: "To Dr. Nikolsky who also struggles with these mysteries". I believe that joint efforts of scientists the world over will eventually do away with numerous mysteries that still have currency in fishery biology and help to organize rational fishery in international waters, a work which Dr. Rollefsen has been contributing greatly to.

CONCLUSIONS

Every animal species is relatively stable in time and space. This relative stability is provided by adaptive intraspecific variability which makes it possible for the species to exist under certain changes of its biotic and abiotic environment. Species is an open self-regulating system. Eurybiont species usually possess a more complex intraspecific structure and a wider range of self-regulation mechanisms than stenobiont species adapted to more stable conditions.

The knowledge of specific structure as well as its regulatory parameters is essential for rational exploitation of commercial species populations and the ensurement of their reproduction. The most essential system of regulatory mechanisms manifests itself in food supply and reproduction rate variability. Disturbances in this regulatory system affect recruitment and bring about a lack in resources of the given commercial species, i.e. overfishing in the biological sense.

An essential regulatory mechanism which secures the existence of the species is an adaptive morphological variability of its specimens. Every year-class is somewhat distinguishable from adjacent year-classes due to the specificity of its living conditions. At the same time adjacent year-classes specifically in the species with a long life cycle mutually interact, affecting the growth rate, fecundity and other year-class characters.

In specific structure the relationships between intraspecific forms is its essential property. To meet the requirements of fisheries, not only the information of the size and properties of the different species forms are essential, but also the possibilities of reproduction of one of the forms by another, i.e. the character of their relationships.

The knowledge of the peculiarities of commercial species regulatory mechanisms and their structure are prerequisite for developing productive fishery.

SUMMARY

The paper presented deals with the problem of intraspecific structure and variability in fishes. Four forms of intraspecific groups are noted. The necessity to study the intraspecific structure and variability for fishery management is emphasized.

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PHYSICAL VARIABILITY IN THE SEA AND THE CONSEQUENCES FOR FISHERIES HYDROGRAPHY

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INTRODUCTION

Fisheries hydrography relies on physical, chemical and biological oceanography and as a marine science tries to solve practical problems in fisheries by understanding the behaviour of various organisms in connection with the natural environment. A broader basis of studies was given by the foundation of the International Council for the Exploration of the Sea (ICES) in 1902. General and detailed facts could be established: the stocks of commercial fish are integrants of ecological systems in which interrelated physical and chemical conditions of great complexity operate and fluctuate from year to year. These systems exercise decisive influence on reproduction, growth and mortality of the organisms, and no rational study of fish can be undertaken without exhaustive inquiry on the physical-chemical conditions. Among the factors of the ecological systems are water temperature, salinity, depth, pressure, currents, content of different nutrients, oxygen, light, osmotic pressure, hydrogen-ion concentration, food (Dietrich, Sahrhage and Schubert 1959). Measuring and understanding of the physical and chemical factors have developed enormously during the last ten years. This is not without influence on fisheries hydrography as such factors have to be taken into account in biological oceanography. New important environmental factors could still be discovered.

The great development in physical and chemical oceanography in the last decade became possible by the introduction of modern electronics to measurements and data processing. Stratification and motions were revealed and showed surprising variations, periodic and non-periodic. Physical oceanography was challenged to measure and to ex-

Contribution given in honour of Gunnar Rollefsen at his 70th birthday.

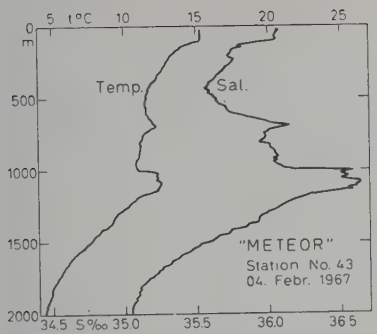

Fig. 1. Vertical profile of temperature and salinity based on a bathysonde record 40 n.m. west of Cap São Vicente ($\varphi = 36°53'N$, $\lambda = 9°50'W$). (After SIEDLER 1968).

plain these phenomena and to give the biological oceanography a base to study the consequences on the behaviour of the species. Under the topic "variability" these processes and their interrelation in space and time became one of the central tasks of present oceanography.

PHYSICAL VARIABILITY IN TIME AND SPACE

What is the meaning of the general term "variability" in the sea? The answer is demonstrated in five examples using the recordings of modern instruments. The first one (Fig. 1) shows the vertical distribution of temperature and salinity with the fine structure of layering. The continuous records were taken during an anchor station of R/V Meteor during the Atlantic seamounts cruises 1967 near Cap São Vincente in the mixing area of Atlantic and Mediterranean water masses. The second example (Fig. 2) shows the variations in time of temperature and current

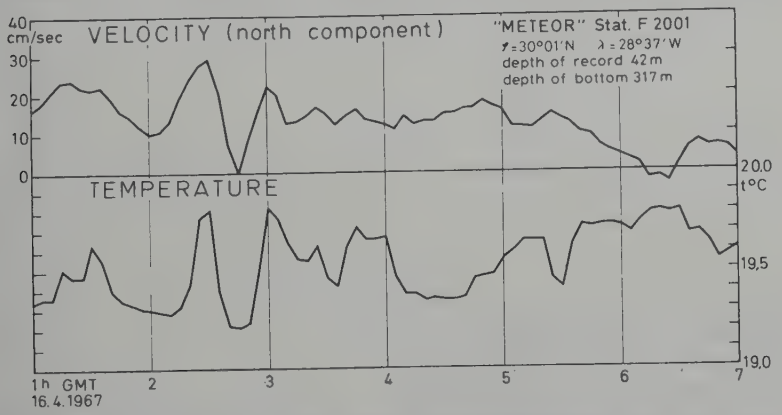

Fig. 2. Time variations in current velocity and temperature on the Great Meteor Seamount over a period of 6 hours. (After MEINCKE 1969).

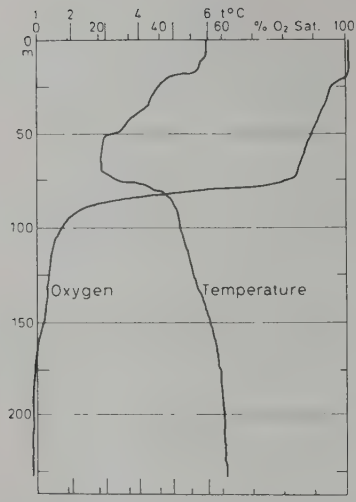

Fig. 3. Vertical profile of temperature and oxygen in % of saturation based on an oxygen–sonde record in the central Baltic 8 May 1968 ($\varphi = 57°03'N$, $\lambda = 19°50'E$). (After Grasshoff 1969).

velocity (north component) recorded from a moored instrument system. This example covers six hours and is a small part of a series of long records in the area of the Great Meteor Seamount, showing that even in the open ocean short term changes govern the current and temperature recordings. In a third example (Fig. 3) the vertical distribution of oxygen and temperature in the central Baltic is presented, showing the fine structure of layering. The oxygen changes from 90% to 10% saturation in a thin discontinuity layer at about 80 m depth. In depths more than 150 m the curve is below the zero line, i.e. hydrogen-sulphide appears in the water. In the fourth example (Fig. 4) is demonstrated that a recording

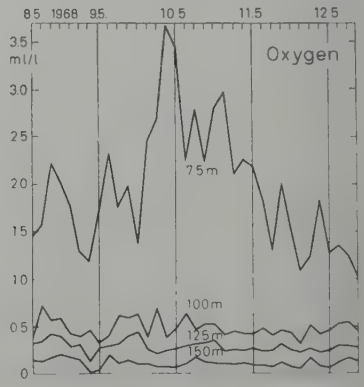

Fig. 4. Time variations of oxygen at different depths during 8–12 May 1968 in the central Baltic ($\varphi = 57°03'N$, $\lambda = 19°50' = E$). (After Gieskes and Grasshof 1969).

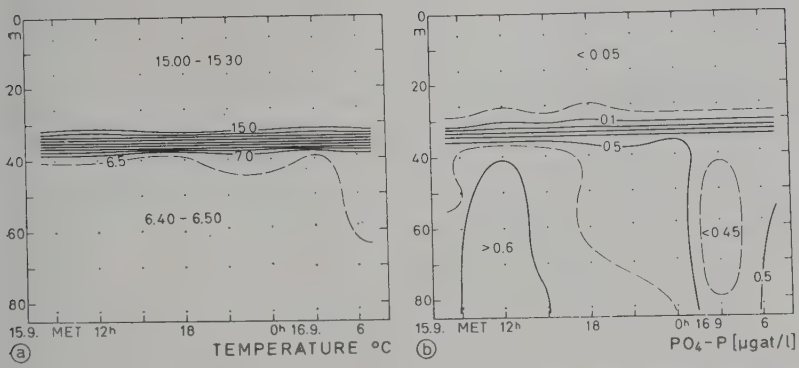

Fig. 5. Time variations during 24 hours, 15–16 Sept. 1968 in the central North Sea represented as isopleths ($\varphi = 56°21'N$, $\lambda = 1°3'E$). (After Ehrhard and Schott 1969).

as in Fig. 3 is not representative, even for some hours. There are time variations in the oxygen content at the same point in the central Baltic. The reasons are vertical movements in internal waves as well as horizontal movements transporting different horizontal water masses which, in the Baltic, are of relatively small dimensions. Such a local inhomogenety of the water can exist in a sea like the Baltic with extremely small tidal currents. But even in the North Sea with strong tidal currents and great mixing short term changes of chemical parameters are pointed out (Fig. 5b) as opposed to the temperature (Fig. 5a). Both figures are based on repeated observations during an anchor station of R/V Alkor. The changes of phosphate content in the deeper layers are about 50% of the absolute value, although the temperature is constant. This means that short term chemical-biological processes exist, which qualify to differentiate between water masses where temperature and also salinity show homogeneous water. Results like these reveal that the sea is much emor complicated in stratification, motion and variations with time than physical and chemical oceanographers had imagined only ten years ago. This, of course, is not without consequences for the fisheries hydrography.

The following facts of common validity may be summarized:

1. The stratification has a rather fine structure, i.e. temperature and salinity may vary strongly in only a few meters of vertical distance. These abrupt changes influence the vertical distribution of currents and chemical parameters and therefore, the environment of the organisms.
2. The fine structure of the stratification changes in time and space.
3. The changes in time consist partly of periodically vertical move-

ments. They are partly unperiodic, and partly they belong to local inhomogeneties in the water.

A single hydrographic station is only representative within a wide range when measuring the fine structure of the vertical distribution of the main physical and chemical components (temperature, salinity, sound velocity, current-shear, oxygen). These measurements must be taken by research ships, since new principles in instrumentation have been developed in the last ten years (bathysonde, sound-velocity meters, current-shear meters, oxygen sonde, etc.).

The observed facts require further special instrumentation to obtain continuous records from moored measuring systems of at least temperature, salinity and current speed and direction. As carriers of instruments different systems are used:

1. Surface buoys damped against surface wave oscillations.
2. Submerged buoys, released from the mooring by an acoustic signal.
3. Masts or posts at the bottom.
4. Underwater winches moving sensors up and down regularly.

The two last systems are usable only in the shelf regions as it was done in the Baltic (Krauss 1960, Siedler and Krause 1967).

By the period analysis of longterm registrations general conclusions can be drawn in spite of the special local characteristics in different areas. Examples from the central Baltic, the central North Sea and the subtropical Atlantic Ocean may illustrate this fact. Figs. 6 and 7 show the amplitude spectra of current velocity components from these records. In Fig. 6 curve a) from the Baltic Sea indicates a significant peak at the

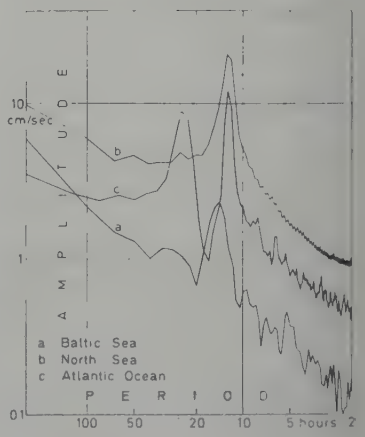

Fig. 6. Amplitude spectra of current velocity, north component, from a) Baltic Sea ($\varphi = 55°3'N$, $\lambda = 13°51'E$), depth of record 39 m, depth of bottom 45 m, 4–25 Aug. 1965. (After Krauss, unpubl. results). b) North Sea ($\varphi = 56°20'N$, $\lambda = 1°0'E$), depth of record 10 m, depth ob bottom 85 m, 14–27 Sept. 1968. (After Schott 1969). c) Atlantic Ocean ($\varphi = 29°60'N$, $\lambda = 28°37'W$) depth of record 50 m, depth of bottom 322 m, 30 April–30 May 1967. (After Meincke 1969).

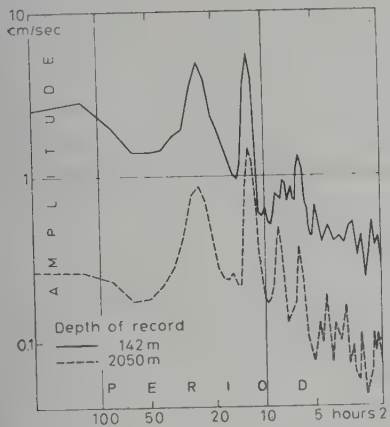

Fig. 7. Amplitude spectra of velocity, north component, from current meters moored by R/V Meteor ($\varphi = 29°05'N$, $\lambda = 29°02'W$, depth of bottom 4630 m, 13–28 April 1967. (After Meincke 1969).

inertial period. Curve b) gives the spectrum from a 14 days-record of the homogeneous upper layer in the central North Sea and shows that the half day-tidal component is the only motion of importance. In curve c) the spectrum from a 30 days-record in the Atlantic measured on top of the Great Meteor Seamount, the tidal periods of 12.4 and 24 hours and the inertial period predominate. Two spectra from different depths of a deep sea mooring with water depth 4630 m (Fig. 7) demonstrate that the spectra may differ on different levels even at the same location.

The general features revealed by spectral analysis are:

1. The amplitudes of motion decline towards shorter periods.
2. Records in close vicinity—vertical as well as horizontal—may show low coherence.
3. Only three main types of motion exist in almost all areas of the sea: the tidal currents of half and one-day periods, inertial oscillation with its latitude-dependent period, and the stability oscillation with a period determined by the density stratification.
4. In addition to these narrow bounded sectors of the period spectrum a multitude of periodic and non-periodic motions of almost unknown origin complicates the picture.

Measurement and interpretation of these processes and of the fine structure of stratification are among the main tasks of modern physical oceanography, and this requires further use of moored systems of instruments.

INSTRUMENTS REQUIRED FOR STUDIES OF THE VARIABILITY

The instruments available for mooring are prepared to record up to two months. A longer time interval is not realistic unless sufficient fouling protections for the sensors are developed. The time interval between two single measurements can be between quasi-continuity and one hour, but further changes are not difficult. The measuring depths desired are mainly down to 500 m, in some cases to the bottom in 5000 m.

The accuracy requirements of the measurements depend on the variability in the ocean areas and may, therefore, only be stated for certain ranges. The necessary high accuracies are not fulfilled in all cases as they can be made available only with great technical efforts, e.g. $\pm 0.01‰$ in salinity or ± 0.01 dbar in pressure:

The standard lower limits of accuracy are:

Temperature	± 0.01 to ± 0.1 °C
Salinity	± 0.01 to $\pm 0.1‰$
Current direction	± 1 to $\pm 5°$
Current speed	± 1 to ± 10 cm/sec
Pressure (gauge)	± 0.01 to ± 0.1 dbar
Pressure (depth)	± 1 to ± 10 dbar.

The attention is focussed on better reliability of the measuring systems under the hard conditions at sea and also on better mooring systems. The methods must be improved, the losses of instruments must be diminished thus increasing the efficiency of the measurements.

CONSEQUENCES FOR FISHERIES HYDROGRAPHY

As demonstrated new sophisticated methods have been developed in physical and chemical oceanography. The progress in fisheries hydrography, however, seems to be inadequate because the correlations between nonbiological and biological factors are not fully understood. Two steps should be made:

1. To study the processes causing the physical and chemical variability.
2. To investigate the biological variability and its relationship to the physical and the chemical variability.

Both can be done in form of experiments in selected areas of the ocean. One of such tests is prepared in the Norwegian Current on the continental slope in autumn 1969 with scandinavian, icelandic and german scientists and with a concentrated effort of research ships and moored re-

cording systems. The results may among other things give criteria, e.g. sampling positions, for moored buoys with data-telemetering systems. Even if no other relationship is known but that between the temperature and the fish distribution such buoys may prove to be as useful as a multinational project of synoptic surveys with research ships as discussed in the ICES and demonstrated by the usefulness of the pilot project in 1966 (Eggvin 1966).

SUMMARY

Progress in fisheries hydrography depends on progress in the knowledge of physical and chemical variability in the sea. This variability is caused by short term changes in the fine structure of layering in temperature, salinity, current and chemical parameters and revealed by the new ways developed in instrumentation. Some examples of the results, achieved in the North Atlantic, the North Sea and the Baltic, are represented.

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THE GAS CONTENT IN THE COREGONID SWIMBLADDER

By

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INTRODUCTION

The gas content in the swimbladder of coregonid fishes has been described from different species and localities by several authors (Hüfner 1892, Saunders 1953, Scholander, van Dam and Enns 1956, Sundnes, Enns and Scholander 1958, Sundnes 1959 and Sundnes 1963). The swimbladder gas in the investigated species is found to contain 99 vol% N_2. The classical example is Hüfner's paper on *Coregonus acronius* Rapp. In *Coregonus lavaretus* (L.), however, the gas composition was different to other investigated coregonids (Sundnes, Enns and Scholander 1958). In this species the O_2 percentage increased with depth as for physoclist fish (Scholander, Claff, Teng and Walters 1951).

Rete structures are found both in the vascularisation of the swimbladder wall of *C. lavaretus* (Fahlén 1959) and *C. acronius* (Fahlén 1967), and there are seemingly no anatomical background for expecting a different gas mixture to be deposited in the two species.

The findings of 15.2 - 18.2 vol.% O_2 in the swimbladder of *C. acronius* in the autumn (Sundnes 1959) and the different distribution of *C. acronius* and *C. lavaretus* with respect to depth (Sundnes 1963) lend support to the theory that the higher nitrogen content in the coregonid swimbladder is a secondary result of the swimbladder physiology. In the present paper a comparative investigation of the swimbladder gas in two coregonid species is presented.

MATERIAL AND METHODS

The species investigated in the present paper are *Coregonus acronius* from Bodensee (Lake Constanze), Germany and *Coregonus lavaretus* from the lake Randsfjord, Norway.

Contribution given in honour of Gunnar Rollefsen at his 70th birthday.

The fish were caught by gillnets at depths varying from 15—35 m in Bodensee, and at 70 m in Randsfjord in October and November respectively. The gas samples were drawn from live fish immediately after reaching the surface. The gas analyses were performed in the 0.5 cc gas analyzer (SCHOLANDER 1947). The O_2 content of the fish blood was analysed in a syringe analyzer (SCHOLANDER and VAN DAM 1956). A few specimen of *C. lavaretus* were transported live to the Institute of Marine Research, Bergen for shallow water experiments.

RESULTS

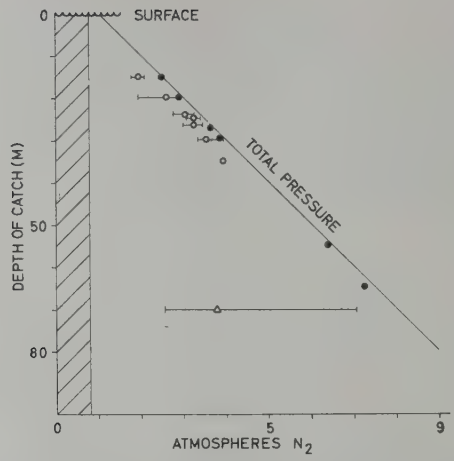
C. acronius was only found in depths down to 35 m probably due to the increasing pollution of the deeper fishing grounds. A single specimen caught at 25 m had a N_2 content in the swimbladder of 98 vol.%. The highest O_2 content measured in *C. acronius* was 33.9 vol.% in a specimen caught at 20 m. Among *C. lavaretus* from 70 m depth in Randsfjord the highest N_2 content was 88.6 vol. %.

The variation in the swimbladder gas content of *C. acronius* and *C. lavaretus* at different depths are shown in Table 1.

Table 1.

Number of fish	Depth in meters	Total range in gas content			
		C. acronius		*C. lavaretus*	
		vol.% N_2	vol.% N_2	vol.% O_2	vol.% N_2
5	15	11.5—28.8	70.8—87.4	—	—
48	20	2.0—33.9	63.4—97.5	—	—
15	24	1.8—17.0	82.3—97.5	—	—
3	25	1.2—12.1	87.5—98.3	—	—
2	27	5.1—17.7	82.8—94.2	—	—
6	30	4.2—14.9	84.4—94.9	—	—
1	35	12.0	87.7	—	—
42	70	—	—	10.6—68.8	30.7—88.6
3	Shallow water aquarium			9.3—25.6	70.4—90.1

The mean values and the range of pN_2 for the two species at different depths are plotted against the total hydrostatic pressure in Fig. 1. The pN_2 in the swimbladder of *C. acronius* caught at different depths in May are also plotted against total hydrostatic pressure. Using average values is not quite correct since the spread of data really reflects different biological situations of the fish.



Figur 1. Mean pN_2 in the swimbladder of coregonids in relation to depth. ● *C. acronius*, May. ○ *C. acronius*, October. △ *C. lavaretus*, November. ⊢⊣ indicate total range. ▨ partial pressure of dissolved N_2 in the lakes.

DISCUSSION

The primary gas deposited into the swimbladder has an O_2 content higher than that of the air. This is definite in *C. lavaretus* which inhabits relative shallow water. During the spawning period it migrates to deeper areas and has a much higher O_2 content than that of air. (Sundnes, Enns and Sholander 1958). A prolonged stay in the deep areas without even small vertical migrations would result in an absorption of the oxygen. It is very unlikely that the oxygen exposed to living tissue in the swimbladder behave like inert gases. The gas will immediately enter the energy metabolism. During a prolonged stay at a certain depth, the O_2 in the swimbladder lost by metabolism will be replaced by a mixture of O_2 and N_2 to keep the fish buoyant at that depth. By a continous replacement of the O_2 partly by N_2, the N_2 content of the swimbladder gas will increase asymptotically. This is seemingly the process in *C. acronius* which is abundant in deeper areas. A similiar process is also possible in *C. lavaretus*, as shown by the high N_2 values in Table 1. Also in shallow water the same situation occur when vertical migrations are possible. *C. lavaretus* kept for 2 months in a 40 cm deep tank had a swimbladder gas consisting of 90.1 vol.% N_2 and 9.3 vol.% O_2.

Like *C. lavaretus* also *C. acronius* is able to deposit a gas mixture into the swimbladder having an O_2 higher than that of air. (Table 1). Due

to the different vertical distribution of the two species (Sundnes 1963), a high O_2 content as found in *C. lavaretus* should not be expected in *C. acronius*.

As an example, a stationary, buoyant *C. acronius* at a depth of 30 m will have a swimbladder gas consisting of about 99 vol.% N_2. By migration to a depth of 10 m, the volume of the swimbladder is kept constant by releasing gas. The gas left in the swimbladder has the same high N_2 content. When migrating back to 30 m, the swimbladder will be compressed to half the volume. To be neutrally buoyant a gas deposition corresponding to half the volume of the swimbladder in that depth is necessary. E.g. a maximum mixture of O_2 like those found in *C. lavaretus* consisting of nearly 70% O_2, will give a maximum O_2 content of 35 vol.% O_2 in the swimbladder of a buoyant *C. acronius*. In the present investigation a O_2 content of 33.9 vol% is found in the swimbladder of *C. acronius*.

CONCLUSION

The present findings support the theory that the high N_2 content found in the coregonid swimbladder is a compensation of the loss of O_2 to the surrounding tissue and not due to a primary deposition of a gas mixture containing a high percentage of N_2.

The replacement of the gas volume is made by a mixture og O_2 and N_2, and the continous loss and replacement function gives an increase in the N_2 content.

The high O_2 content in both species support the theory that the gas is deposited into the coregonid swimbladder from the vascular system of the fish.

The underlaying mechanism of the deposition of gases into the coregonid swimbladder, however, is still an open question.

ACKNOWLEDGEMENT

The present work was made possible by the support of Det Vitenskapelige Forskningsfond av 1919 and Nicolai Andresens Fond. We are indebted to Dr. W. Nümann and his staff for the arrangements at the Institute für Seenforschung und Seenbewirtschaftung, Langenargen am Bodensee. We also wish to thank Mr. A. Göppinger sen. and Mr. A. Göppinger jr. for their services. Our sincerest thanks are also addressed to Mr. O. J. Berger, Jevnaker for his cooperation in securing the material from the lake Randsfjord.

SUMMARY

The present investigation support the theory that there are no differens in the swimbladder physiology of *Coregorus acronius* in Bodensee and *Coregonus lavaretus* in Randsfjord. The high N_2 content found in *C. acronuis* is due to absorption of the O_2 content of the swimbladder.

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NOTES ON THE DISTRIBUTION AND ECOLOGY OF *MYXINE GLUTINOSA* L.

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The hagfish (*Myxine glutinosa* L.) is very common on muddy bottoms along the west coast of Norway, and has for at least 80 years been a favourite subject for anatomical and histological research. Its life history is not, however, correspondingly well known, and although it may live for a long time (several months) in aquaria, it does not breed there. The embryology is practically unknown.

In recent years Foss (1962) has made important contributions to the knowledge of the ecology of the species by discovering its burrows (in Ulvikpollen in Hardanger, West Norway) and by tagging experiments.

The present notes are concerned with the distribution and ecology of the species, based on observations made by the author during 11 years of field work in the Bergen area and the Hardanger Fjord, and also on an analysis of the available literature.

The hagfish has figured in Norwegian scientific literature since the time of Linné, and several authors have taken part in the discussion of its relation to the major systematical groups. (For instance Gunnerus 1763, and Kalm 1753). Krøyer (1852–53) stated that the species is found all along the Norwegian coast, and Nilsson (1855) mentioned its abundance on some parts of the Scandinavian coasts. Collett (1875) said that it is found in all suitable localities along the Norwegian west coast, and Nansen (1886 and 1888) mentioned that several hundred specimens could be collected at Alverstrømmen (north of Bergen) (cf. Brinkmann 1961), and that it is " more common than any other fish " in the fjords around Bergen.

Contribution given in honour of Gunnar Rollefsen at his 70th birthday.

According to Grieg (1914 p. 52), it is found down to a depth of 500 metres around Bergen, is abundant in the Hardangerfjord, and " occurs quite commonly up to about a depth of 10 metres in the innermost part of Jondalsbugten on muddy bottoms ". Tambs-Lyche (1954) found that the species occurred almost everywhere in Sørfjorden and Osterfjorden in North Hordaland, on muddy bottoms up to a depth of about 100 metres.

Throughout its area of distribution, the hagfish is a characteristic animal on the muddy bottoms which cover most of the fjord deeps.

As mentioned above, Grieg (1914) found that the hagfish occurred down to 500 metres around Bergen. In later years, however, it has repeatedly been caught, sometimes in large numbers, at a depth of 690 metres in Korsfjorden near the Biological Station Espegrend; and Lyngnes (1930) mentions catches taken at a depth of 1100 metres in the Sognefjord. At one station (ZF 176) in the Hardangerfjord (Samlafjord near Ålvik), 473 specimens were caught in baited eel-traps at a depth of 864 metres. The greatest depth mentioned by Bigelow and Schroeder (1948) is 524 fathoms (985 metres). One may therefore conclude that there is, at present, no real indication of the maximum depth at which it may be found.

It is also of greater interest to find the upper limit of its occurrence.

As mentioned above, Grieg (1914) found the species " quite commonly " at a depth of 10 metres in Jondalsbukten in Hardanger. In July 1959, the present author thoroughly investigated the locality but was unable to find the species between 8 and 24 metres, from which depth the bottom of the bay descends steeply. In any case the bottom of the bay is not suitable for the hagfish as the mud is mixed with coarse sand and gravel. It is therefore probable that Grieg's statement is erroneous, or perhaps more likely, the figure 10 may be a misprint for 100 metres. The species, in any case, does not occur at the depth stated.

All available information shows, however, that *M. glutinosa* ascends to lesser depths as one passes from the open coast towards the inner fjords. In the relatively open waters of the outer areas, for instance, near the Biological Station Espegrend, it has so far not been caught above 95 to 102 metres (near Ospøya in Raunefjorden), although several attempts have been made to find it in shallower localities where it might be studied. Near Herdla (the site of the Biological Station before 1940), it was known to occur regularly in Ypsøy sound, where the depth varies between 30 and 70 metres (Herdla collecting station No. 12). It is probable that the species was caught at the greater of these depths rather than at the lower. Ypsøy sound is near the " bottom" of the Herdla fjord, and forms a small, rather closed basin with sills at both ends. There is a considerable amount

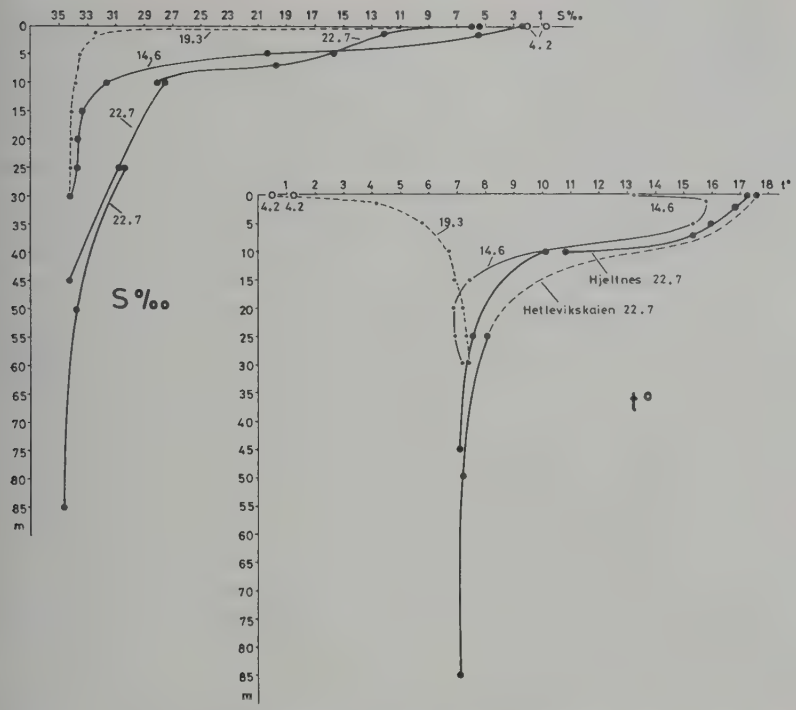

Fig. 1. Hydrographic observations in Ulvikpollen, Hardanger 1959 (July) and 1960 (winter and June). Open rings: winter observations. Filled dots: summer observations. Observations on 22 July were made at three different localities; in the bay proper (bottom at about 15 metres), at the opening of the bay (bottom at about 50 metres), and near Hetlevikskaien (bottom about 90 metres).

of fresh water run off from the nearby Rosselandspollen and from lakes on Holsenøy.

In Ulvikpollen, in the innermost part of the Hardangerfjord, *M. glutinosa* has been caught regularly between 24 and 48 metres in relatively large numbers during the Hardanger fjord investigations (see also Foss 1962). Trials at depths of 9 to 10 metres were always negative.

The available information on the hydrography of Ulvikpollen has been plotted in Fig. 1. It shows that there are large annual variations in temperature and salinity in the layers above 30 metres, but from that depth to the bottom, the temperature and salinity conditions are remarkably constant throughout the year. This figure should be compared with a corresponding one from a locality very similar to the one at Raunefjorden by Burdon-Jones and Tambs-Lyche (1960 p. 19). It shows that

a corresponding stability throughout the year in the outer fjord districts, is found only at a depth of 90 to 100 metres, the minimum depth where *M. glutinosa* occurs in that area.

It may be that a high and constant salinity (32 to 35‰), and also a constant and not particularly high temperature (<about 8°C) are the limiting factors for the distribution of the species. But the physical features of the bottom are evidently also of importance.

Observations of the minimum depth of the species' occurrence in other parts of its area of distribution correspond well with what is known from the Bergen coast.

Krøyer (1852–53) mentions 12 to 20 fathoms as the common depth at which it is found in the Kattegat, and says that it has been found repeatedly at 7 to 8 fathoms. However, Petersen and Levinsen (1900) found it only in trawlings between 300 and 40 fathoms, the only exception being a single specimen caught north of Læsø at a depth of 20 fathoms. Krøyer received his information from fishermen, and their depth figures may not have been so accurate as Petersen and Levinsen's records.

Brattström (1948) found one specimen near Kullen at the northern entrance to Øresund, at a depth of 20–23 metres (length 380 mm.)

Lyngnes (1930) found the species up to 20 fathoms on the Møre coast, and Collett (1875) also mentions 20 fathoms as the minimum depth, while in 1905 he said that it "may be found in shallow bays of only 20 metres depth".

Lilljeborg (1891) mentions 15 fathoms as the upper limit on the Swedish west coast, and Retzius (in Smitt 1875) gives 16 to 17 fathoms as the minimum depth in Gullmarfjorden. Gustafson (1934) mentions 30 metres as the upper limit in the same fjord.

The North Atlantic distribution of *M. glutinosa* extends from Murmansk to Gibraltar. It has been found a short distance east of the Straits of Gibraltar, but does not occur elsewhere in the Mediterranean. It has been found in the Sound (see above), but not in the Baltic. Possibly the salinity is too low. It seems to be more common in the northern part of the area of distribution than in the southern. It has been recorded near the east coast of Iceland at a depth of 940 metres by Konstantinov and Schegolev (1958). Iversen (1936) found two specimens at East Greenland (63°40′N 39°6′W). Fabricius (1780), Krøyer (1852–53) and Jensen (1926) record it in West Greenland waters. The species is also distributed from the Gulf of St. Lawrence (Vladykov 1951) to Delaware Bay and Cape Fear in North Carolina.

Bigelow and Schroeder (1948) compared North American specimens with Norwegian ones, but did not find sufficient difference to consider them as separate, either at the species or subspecies level. They

therefore considered *Myxine limosa* Girard 1859, described from North America, as a synonym for *M. glutinosa*.

There is, however, one difficulty not mentioned by Bigelow and Schroeder. The largest European hagfish recorded were 470 mm (Collett 1875) (from Øksfjord in Finnmarken) and 455 mm long (Nilsson 1955) (from West Norway). The present author, in the course of his stay at Espegrend, measured a total of 1682 specimens from the vicinity of Bergen and the Hardanger fjord, and found the largest animal to be 382 mm long. The average length in most catches was not above 260 to 280 mm. However, a maximum size of 790 mm has been reported from U.S.A., and Conel (1917) mentions a series with an average length of 620 mm.

The size of the animals caught depends to some degree upon the size of the gear used to catch them. At Espegrend, common eel-traps were mostly, but not exclusively used. It may be that some other gear might have caught individuals larger than 382 mm. There is no indication as to the gear used by Conel, but it seems very unlikely that this should be the reason for the great difference in size recorded. It seems therefore worthwhile to make a closer investigation as to the size-distribution of the species on both sides of the Atlantic. If a difference in the maximum size, such as the one mentioned above, is confirmed, that would indicate that at least different subspecies occur in the eastern and western Atlantic.

SUMMARY

The distribution and ecology of the hagfish, *Myxine glutinosa*, in the Bergen area is discussed, especially its depth occurrence. The ascent of the species to lesser depths in the inner fjords is seen in relation to the stability of the water masses. The total distribution of the species is reviewed, and it is suggested that a pronounced difference in size of the animals on both sides of the Atlantic may, if confirmed, indicate that there are different subspecies.

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The author whishes to acknowledge the co-operation of his friends on the staff of the Biological Station Espegrend, in the tiring and not always pleasant work on hagfish.

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ON THE HYDROGRAPHY OF THE SHELF WATERS OFF MØRE AND HELGELAND

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INTRODUCTION

The coastal banks between Stad and Lofoten (Fig. 1) are an important spawning and hatching area for several fish species. The hydrography in this area is, however, insufficiently described, especially the conditions in winter and spring when the spawning and hatching of some of the most important commercial fish species take place.

The topography of the area is presented in Fig. 1. The extension of the shelf in this area is greater than off other parts of the Norwegian coast. In average the width is more than 100 nautical miles, except off Møre where the shelf is narrow.

Basic studies of the hydrography of the coastal banks were carried out by Helland-Hansen and Nansen (1909). Sea surface temperatures in the area were presented by Eggvin (1966), and Ljøen (1962) discussed the hydrography in summer.

The present work presents a description of the general hydrography on the coastal banks in winter. The upper layers are dealt with in detail since their relationship with biological phenomena are of particular interest.

MATERIAL AND METHODS

The analysis is based on hydrographic observations made during two cruises. The first, in February 1956, covered the entire shelf and the adjacent deep sea between Grip and Lofoten (Fig. 5). The second, in early March 1968, covered the shelf between Stad and Frøyabanken (Fig. 7). At all stations observations were taken in standard depths to the bottom, and the temperature at 4 m depth was recorded continuously with thermograph.

Contribution given in honour of Gunnar Rollefsen at his 70th birthday.

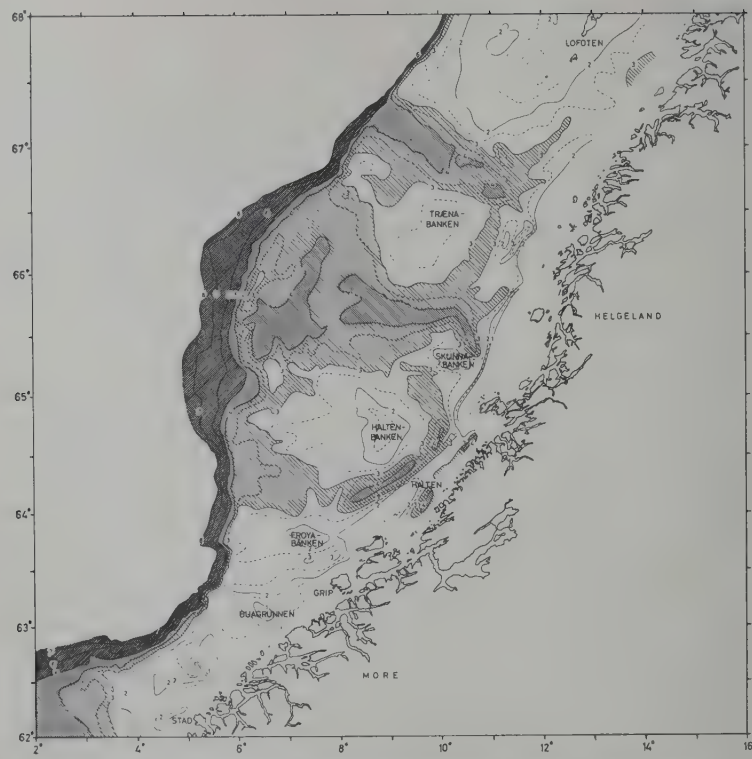

Fig. 1. Bathymetric map of the investigated area. Depths in hectometers.

THE WATER MASSES

Plots of temperature versus salinity from all points of observation are presented in Fig. 2, which gives a view of the different water masses in the investigated area. Three main water masses may be defined: Coast water, Atlantic water and Slope water. The latter is mainly a mixture of Atlantic water and the upper part of the deep water in the Norwegian Sea. The other two, Coast water and Atlantic water, are brought by the currents into the area where their characteristic parameters are altered due to mixing and heat exchange with the air.

Extreme Coast water is characterized by salinities and temperatures lower than 34.5‰ and 5.5°C. A_1 on Fig. 2 represents the core of Atlantic water of the Norwegian Atlantic Current in the southern part of the area. This water is partly protected from direct heat loss to the air by overlying

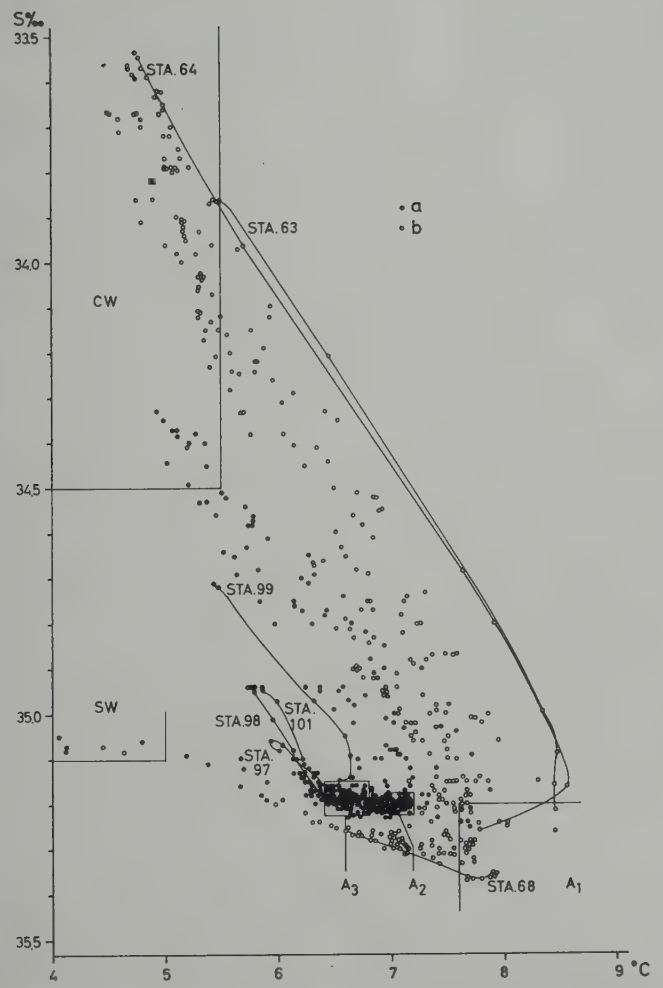

Fig. 2. Temperature–salinity diagram. (*a*) Observations in 1956. (*b*) Observations in 1968. CW: Coast water. SW: Slope water. A_1, A_2 and A_3: Phases of Atlantic water.

Coast water. A concentration of temperature–salinity points around 35.20‰ and 7.0–7.2°C indicates a larger bulk of nearly homogeneous water, A_2, a phase of Atlantic water. This water also gives the main contribution to a water mass, A_3, with salinities 35.15–35.22‰ and temperatures 6.4–6.8°C which have been formed mainly by cooling and a slight mixing with less saline water.

Slope water has salinities and temperatures below 35.10‰ and 5.0°C, and is located at the upper edge of the continental slope. There is no direct connection between Coast water and Slope water.

The temperature–salinity curves in Fig. 2 illustrate clearly that the extreme values of Coast water and Atlantic water are found in the southernmost part of the area. Corresponding to earlier findings (Helland-Hansen and Nansen 1909), both salinity and temperature of Coast water increase further north while the values in Atlantic water decrease. These changes are due to mixing between the water masses and the fact that both masses mainly move to the north.

THE DISTRIBUTION OF TEMPERATURE AND SALINITY

THE 1956 SURVEY

The section

The water mass A_2 is present in a width of 60 nautical miles (between Station No. 70 and 74) and has a thickness of about 250 m (Fig. 3). The water mass is brought into the area by the Norwegian Atlantic Current and makes a trough in the water mass A_3. On the coastal side A_3 is formed as a result of mixing between A_2 and Coast water, and on the offshore side by mixing between A_2 and water from the central part of the Norwegian Sea where the salinity is slightly less than in A_2. The main process, however, underlaying the formation of the mass A_3 in the bankarea, is the exchange of heat with the air. This results in a vertical mixing from the surface to the bottom and a decrease in temperature.

Coast water appears in a narrow zone near the shore. The isohalines slope steeply, indicating a strong northward current relative to the bordering mass.

At Station No. 77 an intermediate maximum in temperature appears with extreme values at 50 and 75 m depths. Originally, this water was of the type A_2, but receives admixture of Coast water in the upper part without significant heat loss to the air.

A ribbon of relatively cold water occurs in the Atlantic phase A_3 in the intermediate and deep layers at Station No. 78. This water has a slightly higher density than the surroundings and is probably formed on Haltenbanken, which partly is shallower than 150 m. Here, the vertical convection from surface to bottom occurs earlier in winter than in the deep waters surrounding the bank.

Another ribbon of relatively cold and less saline water in the Atlantic phase A_2 occurs outside the edge of the shelf. This minimum in the values of the parameters is partly due to an ascent of deep water and not caused by admixture of Coast water.

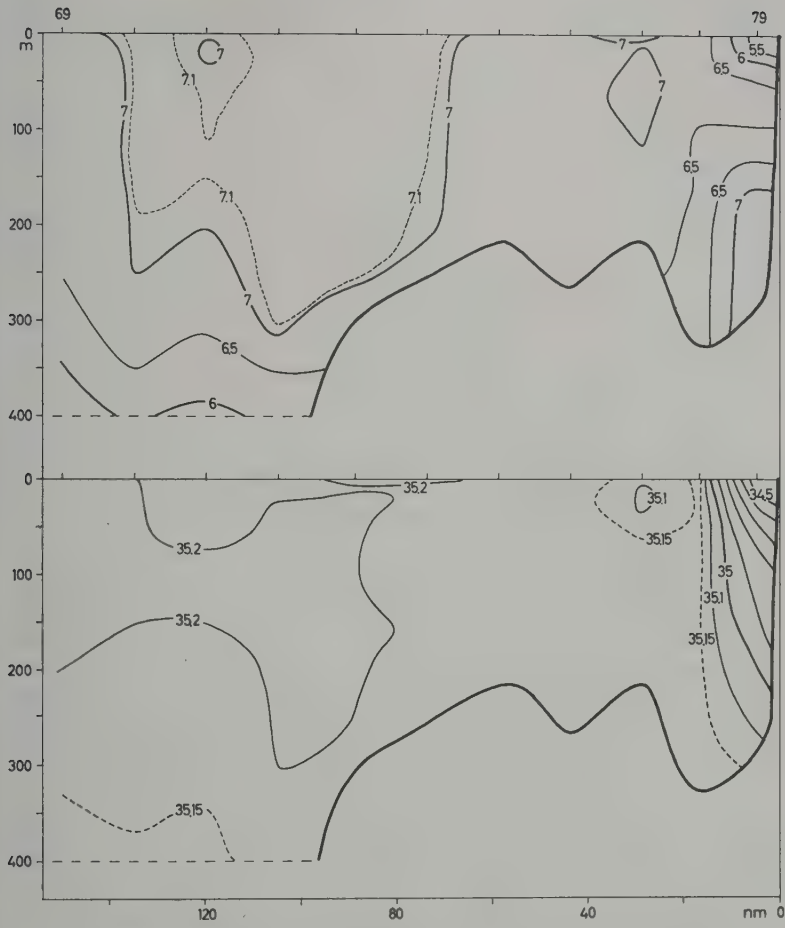

Fig. 3. Temperatures (°C) and salinities (‰) off Halten 20–21 February 1956.

The upper layer

The distribution of temperature at 4 m depth (Fig. 4), recorded continuously, permits more explicit studies than is possible by using the stations only. A change in the temperature in the upper layer is caused by mixing between Coast water and Atlantic water and by heat loss to the air only. The temperature, therefore, is a useful parameter for examination of the distribution of the main masses of the top layer, assuming that the heat exchange with the air is similar throughout the area investigated.

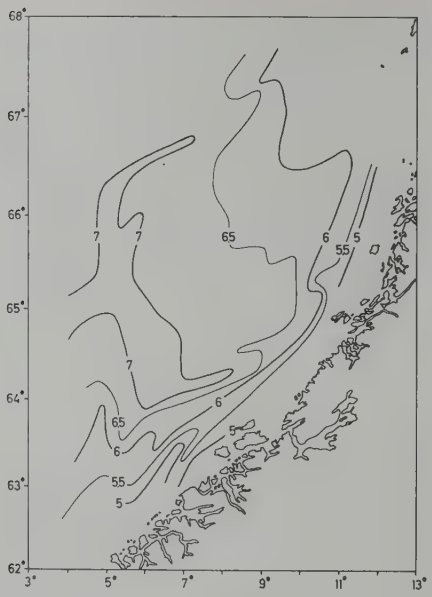

Fig. 4. Temperatures (°C) in the surface layer 18–24 February 1956.

It is evident that the Coast water splits into two branches outside Møre. The main branch runs parallel and close to the coast, whereas the other follows the edge of the continental shelf on top of the Atlantic water. The thickness of this branch was about 50 m in the southern part of the area, but was hardly traceable farther north in the section (Fig. 3).

The Atlantic water seems to move northward along the edge of the shelf, and one branch pushes towards the shore along the channel between Frøyabanken and Haltenbanken.

The intermediate layer

A general characteristic of the Atlantic waters A_1 and A_2 is that high temperature is associated with high salinity (Fig. 5). The distribution of these parameters show that the bulk of these masses moves northwards along the slope, and that two branches are pushed towards the coast in channels between the banks.

The minimum in salinity at Station No. 67 is due to admixture of waters from the outer branch of the coastal water.

The ribbon of ascended water in the phase A_2, mentioned before, gives rise to a minor minimum of temperature above and along the outer part of the slope.

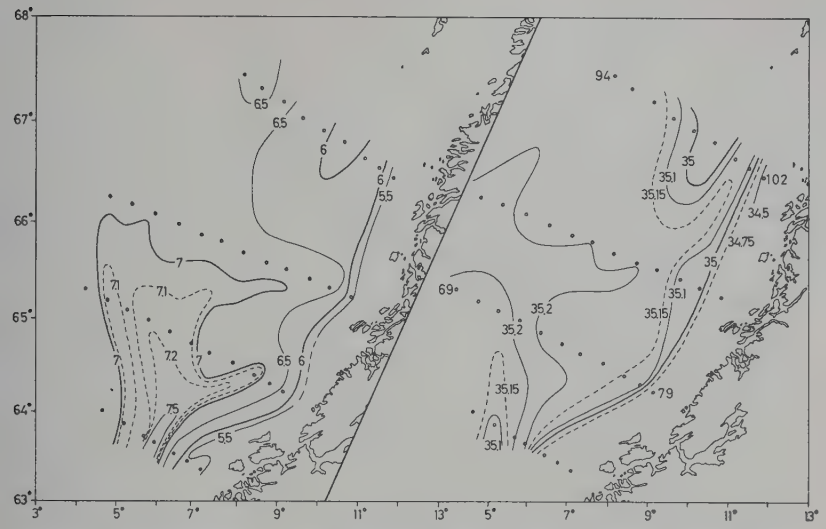

Fig. 5. Temperatures (°C) and salinities (‰) at 50 m 18–24 February 1956. Station grid is indicated.

THE 1968 SURVEY

Observations from 1968 give a more detailed account of the hydrographic conditions in the southernmost part of the investigated area. Fig. 6 shows that Coast water is found across the whole continental shelf as a wedge above the Atlantic water. The extreme values of the parameters in the Atlantic water occur at the inner end of the slope just below the Coast water. The transition layer between the two masses is thin, and

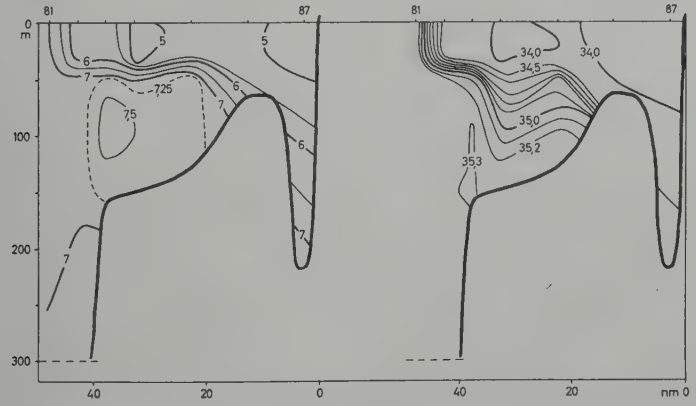

Fig. 6. Temperatures (°C) and salinities (‰) across Buagrunnen 10 March 1968.

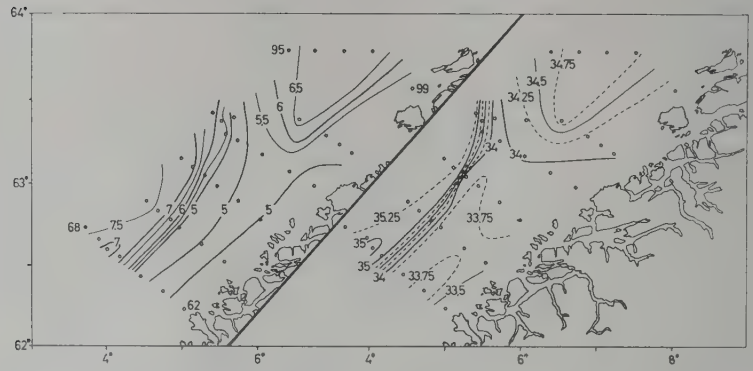

Fig. 7. Temperatures (°C) and salinities (‰) at the sea surface 7–12 March 1968. Station grid is indicated.

relatively large vertical and horizontal gradients occur both in temperature and salinity.

In the upper layer (Fig. 7), above the outer part of the shelf, there is a ribbon of water with low temperatures and salinities which seems to continue northwards along the slope. To the north of Buagrunnen temperature and salinity increase in northward direction.

The distribution of temperature and salinity at 50 m depth is illustrated in Fig. 8. There is a narrow zone of water with temperature maximum following the continental slope. This zone divides into two branches west of Grip. One part follows the continental slope northwards, the other bends to the east and follows the northern slope of Buagrunnen towards Grip.

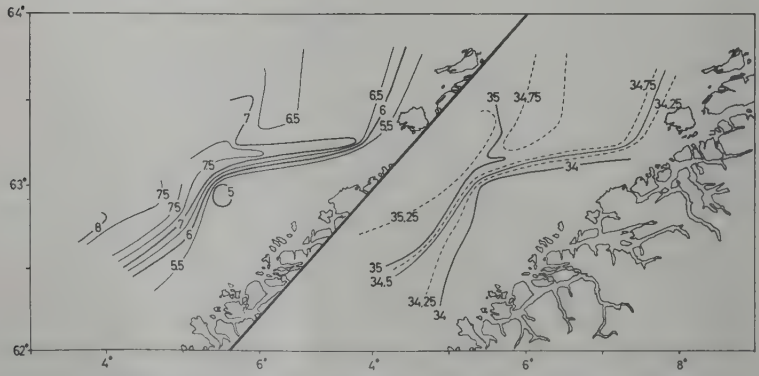

Fig. 8. Temperatures (°C) and salinities (‰) at 50 m 7–12 March 1968.

DISCUSSION AND CONCLUSIONS

From Fig. 2 it may appear as if the temperature and salinity of the Atlantic water were higher in 1968 than in 1956, and that the values of the corresponding parameters of the Coast water were lowest in 1968. This is mainly a geographical variation. The 1968 cruise covered the area where the two water masses recently had come into contact. Therefore, the largest vertical and horizontal gradients were found here. As reported earlier by Helland-Hansen and Nansen (1909), the gradients were smaller farther north due to mixing between these two water masses.

The seaward extension of the Coast water is as a rule larger in summer than in winter (Hjort and Gran 1899). In the summer 1957 (Ljøen 1962), the $35.0^{0}/_{00}$ isohaline at the surface had an average distance of about 150 nautical miles from the shore. The corresponding distance in the winter 1956 was 10–40 nautical miles, except for an area just south of Lofoten. Besides the variation in time also large geographical variations appeared in the extension of Coast water. Off Møre the $35.0^{0}/_{00}$ isohaline intersected the surface at a distance of 40–50 nautical miles from the shore, while farther north, at Helgeland, this distance was only 5–10 nautical miles.

Off Møre the temperature and salinity of the Coast water were lowest at the outer part of the shelf (Fig. 7). This situation supports the suggestion of Helland-Hansen and Nansen (1909) that the northward velocity of the Coast water in this area is greatest at the edge of the shelf. On the main part of the banks the velocities are lower and may have various directions (Dragesund and Nakken 1968). The branch of Coast water which followed the slope northwards from the area west of Buagrunnen also seems to be present in summer (Ljøen 1962, Fig. 4B). The water of this branch mixed in all directions with water masses of higher temperature and salinity and therefore soon lost its original characteristics.

North of Buagrunnen the main bulk of Coast water probably flowed to the east and followed the coast northwards from Grip on. The strongest northward movement of the Atlantic water occurred outside the upper edge of the continental slope. However, there is evidence of a splitting of this current by longitudinal zones with discontinuity in the transversal distribution of the parameters. As in summer (Ljøen 1962), branches of Atlantic water pushed towards the coast in the channels between the banks. This pattern is obviously an effect of the bottom topography.

SUMMARY

1. The distribution of temperatures and salinities off the west coast of Norway have been studied, based on observations from cruises in February 1956 and March 1968.

2. The main flow of Coast water follows the edge of the shelf between Stad and Grip. West of Grip it divides into two branches. One follows the slope northwards, the other flows to the east and follows the coast northwards.

3. The Atlantic water follows mainly the slope, but branches of Atlantic water move to the east in the troughs between the banks.

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THE EFFECT OF FISHING ON SIZE COMPOSITION AND SEX RATIO OF OFFSHORE LOBSTER STOCKS

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INTRODUCTION

The initial effects of exploitation on marine stocks seldom have been thoroughly documented, because the stocks usually are not studied until a species has experienced a history of exploitation. The fishery for lobsters, *Homarus americanus*, in offshore waters of southern New England offers an opportunity to record the chronological changes due to exploitation. The fishery is in the early stages of development and fishing effort is expended disproportionately on relatively discrete grounds.

In this preliminary account of the data collected from the offshore fishery, I compare the size distribution and sex ratio of lobsters from several fishing grounds, and hypothesize that the differences are due mainly to fishing. The hypothesis was developed on the basis of work on sex ratio of lobsters by Thomas (1955) and from data on size distribution collected from research cruises. Data are not yet available, however, on such aspects as seasonal migrations and total catch and effort by area, which must be considered if the effects of fishing are to be fully assessed.

THE OFFSHORE LOBSTER FISHERY

The history of the fishery for offshore lobsters has been reconstructed by Schroeder (1959). Lobsters were taken incidentally in the bottom trawl fishery for various species of groundfish in the early 1900's. In ensuing years, effort was expended specifically for lobsters, but catches through 1946 were less than 50 metric tons. Skud (in press) described the recent increase in landings, which surpassed 500 metric tons in 1955

Contribution given in honour of Gunnar Rollefsen at his 70th birthday.

and 2500 metric tons in 1965. Fishing is conducted with a standard bottom trawl to the edge of the continental shelf, 100 to 400 km offshore, and is concentrated at depths between 100 and 500 meters. The use of the bottom trawl and the depth of fishing are in sharp contrast to coastal fisheries where lobsters are captured in pots, usually at depths less than 50 meters.

The offshore fishery is concentrated near submarine canyons at the edge of the continental shelf (Fig. 1). Five of these canyons have been sampled more intensively than others and can be grouped into three categories by distance from major ports of landing. Hudson and Veatch Canyons are 200 to 250 km offshore, Oceanographer and Lydonia between 250 and 300 km, and Corsair Canyon is about 400 km from the nearest port. Though historical catch records were not tallied by canyon, the canyons closest to shore generally have been fished more heavily than more distant canyons during the development of the fishery. In my analysis, I occasionally combined data from canyons that were equidistant from shore and that had lobsters of simliar size.

Samples were drawn from commercial landings; interviews with vessel captains provided information on the vessel, gear, area and depth of fishing, days fished, and total catch in pounds. At least 100 lobsters were measured and sexed in each sample. (Unless otherwise noted, all measurements refer to carapace length.) Data from research cruises included hydrographic data, time, distance, and the range in depth of each trawl tow. Sampling was concentrated in areas regularly fished by the commercial fleet. Each lobster was sexed, measured, and weighed, and the number of berried (egg-bearing) females was recorded. Research cruises provided information on prerecruits which was not available from commercial landings. Though the fishery operates in international waters, state laws apply to the landings; offshore catches are therefore subject to minimum size (approximately 8 cm) regulations that control the inshore lobster fishery.

CATCH PER UNIT OF EFFORT

To test the generalization that more distant canyons were less intensively fished, catch and effort of commercial vessels were compared by canyon. Effort was measured in days fished —length of the total trip, less fishing days lost. A vessel may fish at several canyons during a single trip but only those trips during which effort was concentrated in the vicinity of one canyon were compared. Further, the comparison was limited to vessels which had fished on at least two occasions in both areas being compared.

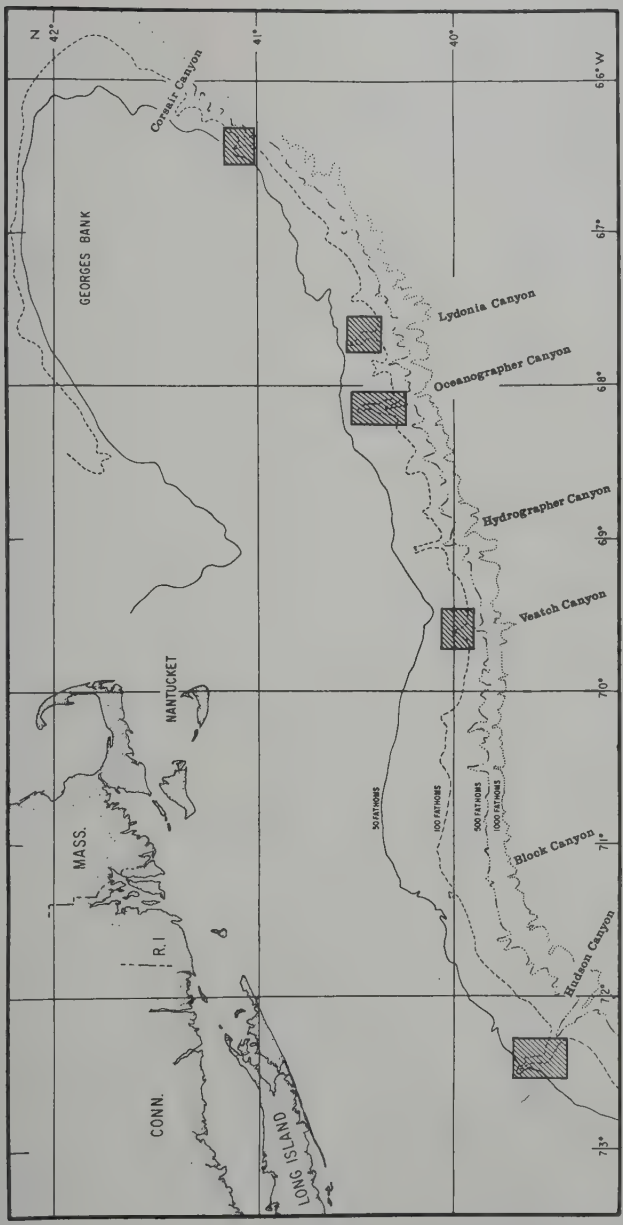

Fig. 1. Sampling locations for lobsters on the continental shelf off New England.

These criteria restricted the selection to six vessels, but included 63 interviews or trips. The average catch per day or catch per unit of effort (CPE) for each trip was determined for each vessel (Table 1). The mean CPE for the vessels ranged from 451 to 621 kg (average, 552) in the Hudson–Veatch area, from 539 to 706 kg (average, 670) in the Oceanographer–Lydonia area, and from 680 to 801 kg (average, 741) in Corsair

Table 1. Average daily catch (kilograms) of lobsters by six vessels in the offshore canyons, 1965–1967. [Entries in the table are the averages for each fishing trip.]

Canyon area	Vessel						A–F
	A	B	C	D	E	F	
Hudson-Veatch	363	665	389	794	486	499	
	605	806	455	303	616	403	
	377	340	713	907	489	—	
	455	340	766	831	756	—	
	562	737	—	495	583	—	
	357	455	—	395	455	—	
	499	377	—	—	455	—	
	801	—	—	—	368	—	
	1264	—	—	—	544	—	
	314	—	—	—	523	—	
	—	—	—	—	455	—	
	—	—	—	—	455	—	
	—	—	—	—	756	—	
Mean CPE	560	531	581	621	534	451	552
Number of trips	(10)	(7)	(4)	(6)	(13)	(2)	(42)
Number of days fished	(77)	(30)	(17)	(19)	(85)	(9)	(237)
Oceanographer-Lydonia	—	826	495	—	529	777	
	—	624	583	—	480	1021	
	—	484	—	—	907	777	
	—	—	—	—	624	907	
	—	—	—	—	990	428	
	—	—	—	—	—	837	
	—	—	—	—	—	408	
	—	—	—	—	—	324	
	—	—	—	—	—	706	
Mean CPE		645	539		706	687	670
Number of trips		(3)	(2)		(5)	(9)	(19)
Number of days fished		(17)	(18)		(36)	(62)	(133)
Corsair	—	—	—	—	—	680	
	—	—	—	—	—	801	
Mean CPE						741	741
Number of trips						(2)	(2)
Number of days fished						(16)	(16)

Canyon (only two trips, 16 fishing days, available for comparison). CPE at Hudson–Veatch, the area closest to the coast, was lower than at more distant canyons.

Assuming that the population densities at the canyons were comparable prior to exploitation, this trend in CPE indicates a more intensive exploitation at the canyons closest to shore. Though early records of total catch and effort are not available to establish this premise, the statistics now being collected and subsequent changes in CPE may help determine the distribution of past fishing effort. The size composition data in the following section do lend support to this thesis.

SIZE COMPOSITION

The mean size of lobsters was related to the distance from shore. Length-frequencies of lobsters were smallest at Hudson and Veatch Canyons, intermediate at Oceanographer and Lydonia Canyons, and largest at Corsair Canyon (Fig. 2). This trend in size follows the expected diminution from fishing, i.e., Hudson and Veatch Canyons lie closest to the coast and presumably have been more intensively fished. CPE was lowest at the Hudson–Veatch area, higher in Oceanographer–Lydonia, and highest at Corsair Canyon.

The data from Veatch Canyon are more extensive than those from the other canyons, and show marked changes in size composition during the three years of sampling. The cumulative percentage of catch of

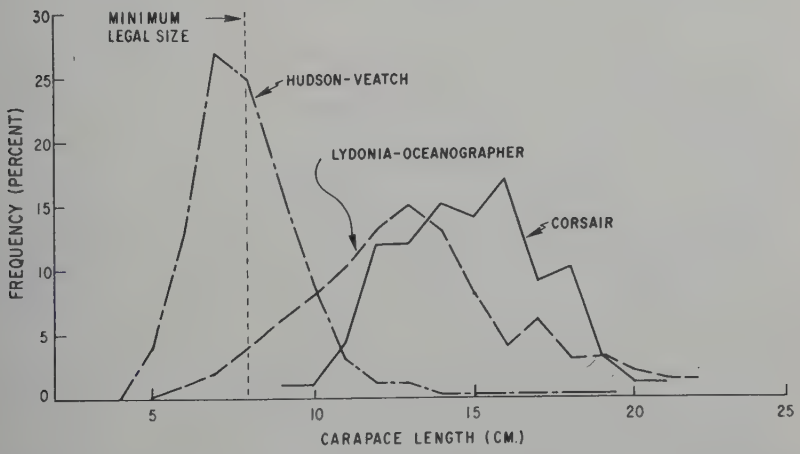

Fig. 2. Length-frequencies of lobsters in catches by research vessels at offshore canyons, 1965–67.

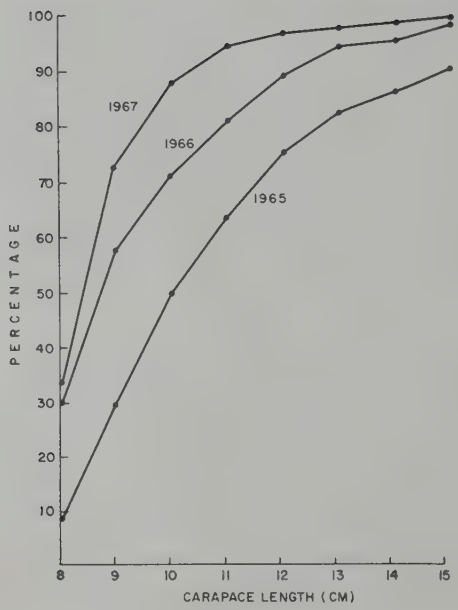

Fig. 3. Cumulative percentage of the catch of legal-sized lobsters at Veatch Canyon, 1965–67.

lobsters 8 cm and larger showed that smaller lobsters accounted for progressively more of the catch (Fig. 3). For example, the percentage of lobsters in the 8 to 10 cm size group was 50 in 1965, 70 in 1966, and nearly 90 per cent in 1967. This progressive change is assumed to be caused by fishing.

Additional evidence that differences in size distribution are related to fishing was obtained by comparing the present data with that reported by McRae (1960) from exploratory cruises made 10 years ago. The modal size of lobsters from Veatch and Lydonia Canyons was smaller in 1965–67 than in 1956 and the decrease in size was greatest in Veatch Canyon which is closest to shore (Fig. 4). The depth of water in which samples were taken ranged from 200 to 500 meters in 1956, however, and from 100 to 300 meters in 1965–67. Since the size of lobsters generally increases with depth, the differences in depth fished in the two periods have contributed to the apparent change in size distribution (Skud and Perkins, in press). To examine this relationship of size with depth, data from recent research cruises have been grouped by depth for comparison (Table 2).

The maximum increase in size with depth was 1.1 cm, whereas the difference in size between canyons was as much as 6.7 cm. Thus a

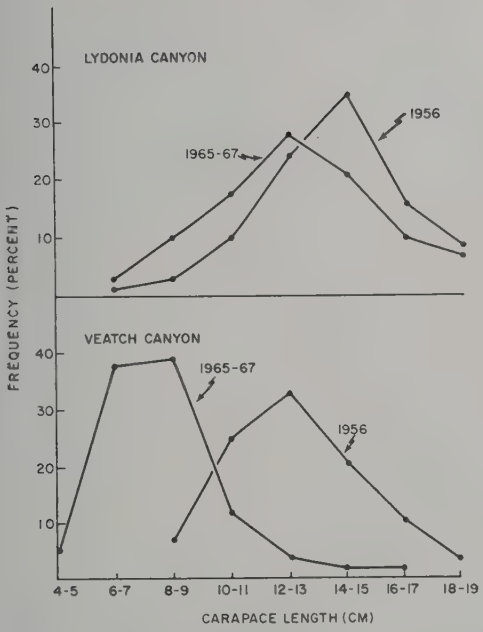

Fig. 4. Comparison of length-frequencies of lobsters collected in 1956 and in 1965—67 at Veatch and Lydonia Canyons.

Table 2. Average carapace length of lobsters by depth of capture.

Canyon	100–200 meters Mean size (cm)	200–300 meters Mean size (cm)
Hudson–Veatch	8.0	8.7
Oceanographer–Lydonia	11.9	13.0
Corsair	14.7	15.4

factor other than depth accounted for most of the difference between the size distribution of the lobsters in 1956 and 1965–67.

Templeman (1936) and others have correlated size of lobsters with temperature and undoubtedly the growth in offshore stocks can be similarly affected. However, it seems unlikely that temperature differences could account for the magnitude and the progressive nature of the changes in size recorded at the canyons.

SEX RATIO

Thomas (1955) constructed a model of a lobster population with a uniform mortality rate, and showed the expected change in sex ratio with size (Fig. 5). The model assumed that mature females molted

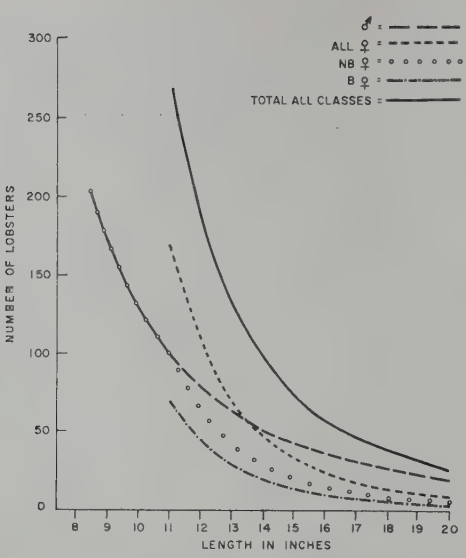

Fig. 5. Size comparison in a model stock, based on a uniform recruitment of 100 males and 100 females at a maturity size of 11 inches (total length) and a 30% total mortality rate. B = berried; NB = Non-berried. (After Thomas 1955).

only once in 2 years, whereas males molted every year. Biennial molting by females was reported by Garman (1892) and later supported by Herrick (1896) and others. Exceptions do occur but Wilder's (1953) data showed clearly that the proportion of non-molting females increases with size at or near maturity. He also showed that males do not always molt annually. Nor is the molting cycle consistent in the offshore populations, particularly in the largest individuals (15 cm or more) that may molt but once in 3 years. However, I do not consider these exceptions as a serious defect of the model, for regardless of the source, the data indicate that, collectively, males molt more frequently than females.

In the model, the sex ratio of immature lobsters is assumed to be 1 : 1. After maturity, the less frequent molting of females causes them to outnumber males at any given size. For example, mature females at 8 cm would remain in this size category and be joined by previously immature females that had molted, whereas males at 8 cm would have molted and progressed to the next size group. If no mortality occurred for either sex, and if all females matured at precisely 8 cm, the ratio of females to males would double at that size. In actuality, all females do not mature at the same size and, as natural and fishing mortality reduce the numbers, the proportion of females increases gradually and the sex ratio can never be expected to reach 2 : 1 (Fig. 6).

Growth rate also influences the observed changes in sex ratio. In

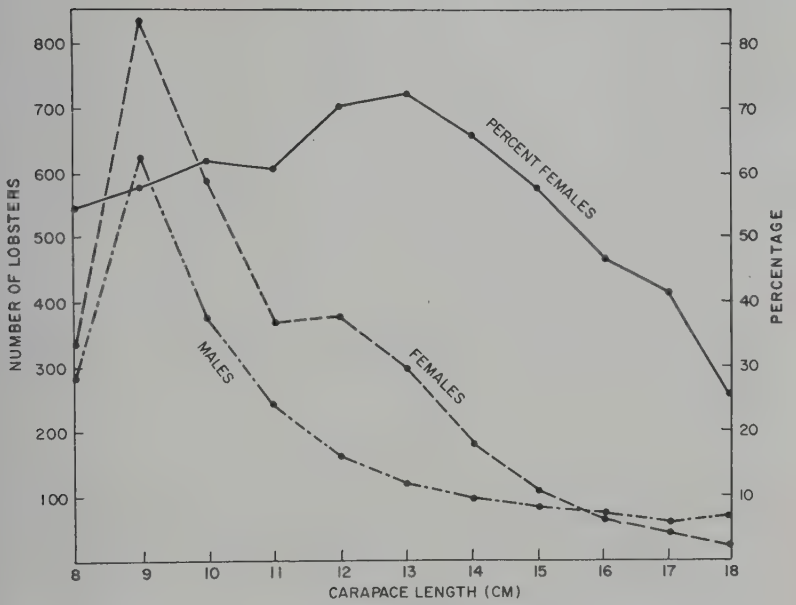

Fig. 6. Numbers of males and females and percentage of females in commercial samples from Veatch Canyon, 1965–67.

the model, the growth increment per molt was considered to be 14 percent. For the offshore lobsters, preliminary estimates showed that growth between molts was 15 percent for mature females, whereas, the increment for mature males was 18 percent. Templeman (1936) also observed differences in growth between the sexes after maturity. This difference concentrates the number of females in smaller length classes and the slower growth, coupled with the less frequent molting, results in an increase in the proportion of females at given sizes.

The increased number of females over males with size is apparent in offshore lobster stocks and can be followed over a greater size range than in coastal stocks (Fig. 6). The increase in the proportion of females with increasing size does not continue indefinitely, but the decline in the rate of increase depends on the rate of mortality. Thomas (1955) concluded that the change in sex ratio could be used to estimate mortality and showed the expected differences in sex ratio in two models, one with a total annual mortality of 70 percent and another with a 30 percent mortality. When annual intermolt mortality of males is 70 percent, mortality between biannual molts of mature females is 91 percent. Or,

if mortality is 30 percent for males, the intermolt mortality of females is 51 percent.

In offshore lobster stocks the proportion of females continues to increase until 12 or 13 cm. In the model the proportion of females was highest at a size class 2 or 3 cm smaller than in the offshore stocks; the difference suggests that offshore lobsters mature at larger sizes than that assumed in the model. However, it is possible to compare the decline in the percentage of females (larger than 13 cm) in the offshore stocks with the changes of sex ratio in the model. The rate of decline at Veatch Canyon most closely approximates that of a 50-percent annual mortality, whereas that from Oceanographer and Lydonia conforms most closely to a 30-percent mortality; these rates suggest a 20-percent greater fishing mortality at Veatch Canyon, if the natural mortality in the two areas is equal (Figs. 6 and 7).

RECRUITMENT

Cole (1954) provided an excellent summary of "population consequences" expected from changes in birth rates and death rates. Under exploitation, he listed three expected changes: (1) a decrease in longevity; (2) an increase in the population's birth rate; and (3) the obvious in-

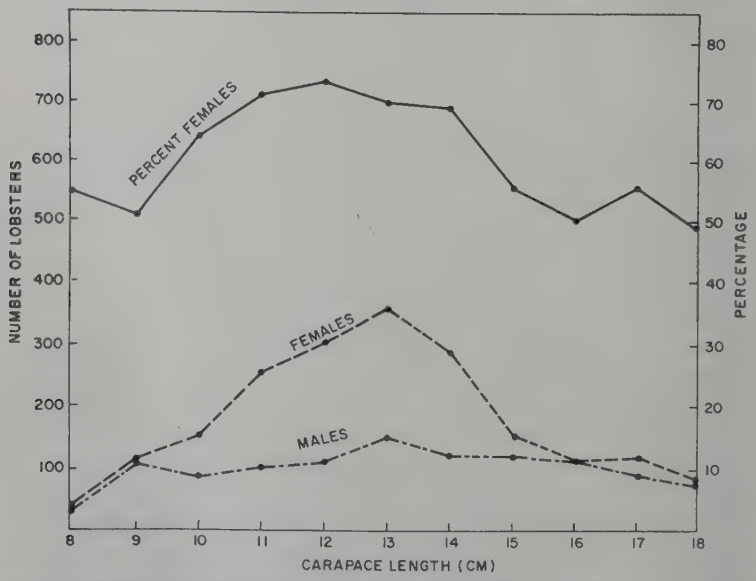

Fig. 7. Numbers of males and females and percentage of females in commercial samples from Oceanographer and Lydonia Canyons, 1965—67.

crease in the proportion of young. Items 1 and 3 are demonstrated clearly in the length-frequencies of lobsters presented earlier, and also from the data on catch per unit of effort (CPE). The average weight of legal-sized lobsters from Hudson and Veatch Canyons approached 1 kg; conversion of the mean CPE (552 kg) from weight to numbers indicated a catch of over 500 lobsters per day. At Oceanographer and Lydonia Canyons, where the average weight was about 2 kg, the converted CPE (670 kg) was 335 lobsters per day. Lobsters at Corsair Canyon averaged 2.7 kg and the converted CPE (741 kg) was 257 lobsters per day.

Item 2, an increase in the birth rate, is difficult to measure in the offshore fishery. Increased birth rate in a population may be reflected in changes of the age or size at first maturity. For lobsters, such a change can be measured by comparing the number of egg-bearing (berried) females to the total number of females at a given size. I have tallied the percentage of berried females taken during the research cruises in 1956 (from McRae 1960) and 1965–67 (Table 3). In 1956, no females were berried at 8 or 9 cm and less than 20 percent were berried at 10 and 11 cm. In 1965–67, a few females were berried at 8 cm, over 20 percent at 9 cm, and more than 30 percent at 10 and 11 cm. This change, which could be due to an increased growth rate, may indicate an increased birth

Table 3. Percentage of berried lobsters among females of different size groups collected in canyons off New England during exploratory cruises in 1956 and research cruises in 1965–67.

Length (cm)	1956		1965–67	
	All females (Number)	Berried females (Percent)	All females (Number)	Berried females (Percent)
6	0	0.0	363	0.0
7	2	0.0	464	0.0
8	12	0.0	441	1.6
9	31	0.0	343	22.7
10	45	11.1	232	33.2
11	122	18.9	133	30.8
12	98	25.5	168	25.6
13	191	35.1	163	27.0
14	131	35.1	121	30.6
15	225	31.1	94	29.8
16	134	26.9	64	37.5
17	52	32.7	46	19.6
18	36	38.9	40	40.0
19	11	45.5	16	18.8
20	3	33.3	3	66.7

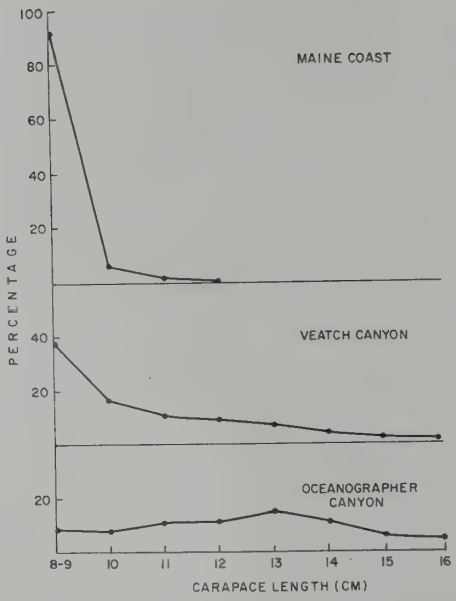

Fig. 8. Size composition of lobsters from inshore and offshore areas (both sexes).

rate and suggests that the increasing proportion of small lobsters in the offshore catches is not only the result of cropping the larger individuals. However, additional information is necessary to determine whether total egg production has increased or whether the improved recruitment of immatures and young adults has been influenced by other factors such as emigration.

COMPARISON WITH THE COASTAL POT-FISHERY

The inshore lobster fishery in Maine is very intense; at the peak of the fishing season more than 4,000 fishermen (including 2,000 part-time) fish more than 750,000 lobster pots. Dow (1964) estimated that recruit lobsters (8 to 9 cm) accounted for 80 to 90 percent of the Maine landings (Fig. 8). The size distribution in the coastal waters is in sharp contrast to that of lobsters offshore, even in the most intensively fished areas. In canyon areas that are fished less intensively, recruits account for only 5 percent of the catch and the dominant size group at some canyons is 13 cm or more.

The proportion of females in the inshore fishery is seldom more than 51 or 52 percent. I examined the sex and size data from 2,500 lobsters

collected along the Maine coast.[1] In the size class from 8 to 10 cm, the proportion of females was 49.8 percent, whereas in the 11 to 12-cm size group only 45.1 percent were females. Male and female lobsters of over 11 cm accounted for only 4 percent of the sample.

The relatively low proportion of females at sizes from 8 to 12 cm and the small contribution of lobsters over 11 cm in the inshore sample are consistent with a total mortality of 90 percent in THOMAS' (1955) model and confirms Dow's (1964) estimate. The model shows an expected 52 percent females in the 10-cm size class, and shows that only 5 percent of the population remains at the next molt (approximately the 11-cm size class). The proportion of females at 11 cm is higher in the Maine sample than the model predicts, but this proportion may be influenced by the release of berried females that are protected by law.

Exploitation of the Maine fishery is apparently so high that there is little or no increase in the proportion of females. TEMPLEMAN's (1936) data from the coastal fishery at Seal Island, Nova Scotia does show a moderate increase in the proportion of female lobsters between the 7 to 10 cm length classes. The proportion of females increased to 58 percent at 10 cm and then declined. The sample excluded berried lobsters, which suggests that the increase was greater than indicated; and this exclusion precludes any detailed comparison with the model. However, the changing sex ratio with size does conform and the proportion of females at 10 cm would indicate a fishing intensity less than that in Maine but greater than that offshore.

SUMMARY

The lobster fishery in the offshore waters of southern New England is in the early stages of development. The assumption that canyon fishing grounds closest to shore are the most heavily fished was supported by a lower catch per day (CPE), a smaller mean size, and a higher total mortality than exists in more distant canyons.

At Hudson and Veatch Canyons, less than 250 km offshore, the average CPE was 552 kg; Oceanographer and Lydonia Canyons extend 300 km offshore and had a CPE of 670 kg; and at Corsair Canyon, which is 400 km from shore, CPE was 741 kg. Lobsters were smallest at the canyons which were closest to shore and had the lowest CPE. The size frequency was higher at the canyons of intermediate distance and the CPE was higher. The largest lobsters were from Corsair Canyon, which is the furthest from shore, and had the highest CPE.

The modal carapace length of lobsters at Veatch Canyon was over 12 cm in 1956 and is now less than 9 cm. In three successive years of

[1] Data provided by JAMES THOMAS, Maine Department of Sea and Shore Fisheries.

sampling (1965–67), the contribution of small lobsters has increased and in 1967 more than 90 percent of the legal-sized lobsters were from the 8 to 10 cm length class. The progressive change at Veatch Canyon and magnitude of size differences among canyons are greater than expected from the influence of temperature or depth of fishing.

Observed changes in sex ratio support the basic assumptions made in THOMAS' (1955) model and follow the expected changes at different levels of mortality. The proportion of females to males increases gradually from 8 cm to 13 cm and then declines. Because females molt less frequently than males, their numbers at a given size decline more rapidly. The model assumes that females molt only every two years; whereas, males molt annually and have a lower intermolt mortality. The change in sex ratio was used to estimate mortality in the offshore fishing grounds. The more distant canyons had a lower mortality, higher catch per unit of effort, and larger size composition. The size composition and sex ratio of coastal lobster fisheries indicated that exploitation was more intense than in offshore fisheries.

The increased proportion of young lobsters in the offshore catches followed expected changes from exploitation, but also suggested an increase in the population birth rate. This possibility was supported by the observation that in ten years the percentage of berried females at smaller sizes of maturity had increased substantially. However, additional data are needed to determine whether the improved recruitment has resulted from other factors.

Additional data and analyses are needed to test the hypothesis that fishing has caused the changes in size composition, sex ratio, and catch rates. If the assumptions hold and the level of fishing continues or increases, the more distant canyons are expected to experience changes in lobster size, sex ratio, and catch rates—comparable to those at the canyons closest to shore.

The size at maturity, frequency of molting, and rate of growth used in the model are not entirely consistent with observations in the offshore fishery. However, the basic concepts seem applicable and the necessary adjustments and corrections can be incorporated into the model when sufficient data are available.

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DATA ON LIFE HISTORY AND CHARACTERS OF *GALEUS PIPERATUS*, A DWARF SHARK OF GOLFO DE CALIFORNIA[1]

By

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INTRODUCTION

The purpose of this paper is to amplify information on the life history and characters of *Galeus piperatus* Springer and Wagner, a dwarf cat shark that has just recently been described from an oceanographically distinctive area in the northern part of Golfo de California, on the Pacific side of northern Mexico. In a way, this contribution supplements the recent account (Hubbs, Iwai and Matsubara 1967) of an even smaller, pelagic, squaloid shark, *Euprotomicrus bispinatus* (Quoy and Gaimard).

Galeus piperatus was described by Springer and Wagner (1966) from two adult females only 296 and 302 mm in total length and one immature female 256 mm long, all from a series of five specimens trawled in Golfo de California. The capture of the type specimens had been discussed by Lavenberg and Fitch (1966) under the name of *Galeus* sp., and the species has been briefly diagnosed with a copy of the original figure by Kato, Springer and Wagner (1967, p. 23, fig. 4), who have assigned it the vernacular name, "peppered shark". For this supplementary account of the species we have had available, in addition to the two mature female types and one additional adult female, three adult and two early juvenile males, and one egg case that, we believe, pertains to this species (Table 1). The types were taken in 1964 by the R/V Alaska of the California Department of Fish and Game; all other specimens, in 1967–1969, by the R/V Velero IV of the University of Southern California, and the research vessels Thomas Washington and Ellen B. Scripps of the Scripps Institution of Oceanography.

[1] Contribution from the Scripps Institution of Oceanography, University of California, San Diego (La Jolla, California 92037).

Contribution given in honour of Gunnar Rollefsen at his 70th birthday.

HABITAT

All known specimens of *Galeus piperatus* have been taken in the northern part of Golfo de California, in the Salsipuedes basin—in a region that is well known for a rather high incidence of endemism and for extreme fluctuations in physical parameters: the annual temperature range of surface waters is extreme (warm like tropical waters in summer, as cool as southern California waters in winter); tidal currents are strong; and vertical and horizontal turbulence are exceptional (Roden 1958 and 1964, Roden and Groves 1959, Hubbs and Roden 1964). The species has not been taken by recent trawling in other parts of the Gulf, nor along the open coast of the Baja California peninsula, nor along the coast south of the Gulf. However, it should be looked for in those areas.

The region where this shark occurs is not only one of considerable endemism, but is also one where a number of northern (warm-temperate) fishes and other organisms occur, apparently as Pleistocene relicts, sympatrically with a reduced assemblage of tropical forms (Walker 1960). Thus, although the fauna of the whole Gulf is largely to be characterized as depleted-tropical, the occurrence of this scyliorhinid in the upper part of the Gulf is not wholly inconsistent with Springer's indication (1966, pp. 583–584) that the "cat sharks appear very rarely in warm waters and inhabit shore waters only in the higher latitudes or in comparatively cool-water areas". The group appears to be mildly anti-tropical, using this term, as originally proposed (Hubbs 1952), to include subtropical and warm-temperate species.

The specimens have been taken through a wide range of bottom depths, from barely over 400 m to hauls at 732–1215 m and 1097–1326 m (Table 1). Similarly, a new hagfish (*Eptatretus* sp.) has been trawled in the same area repeatedly, but nowhere else, at depths from 198 to 1180 m, over a far greater bathymetric range than that inhabited by any of the six other myxinoids we have been collecting in large quantity in Baja California and the Gulf.

Some of the ship records have indicated that this shark at times may enter the midwater zone, in this area of great vertical turbulence. The three type specimens and two others that were misplaced were taken in a large midwater trawl that reportedly was fishing at a depth of approximately 275 m (Springer and Wagner 1966), but Lavenberg and Fitch (1966, pp. 92–95) have stated that the trawling depth for the station was determined as 275 m by measuring the cable angle and ship speed [a dubious determination, especially in an area of notoriously fast currents]. They added that the Precision Depth Recorder during the trawling "showed a constant bottom depth of 220 fathoms (400 m)" — close to the

Table 1. Collection data on known specimens of *Galeus piperatus*.

Specimen no.[1]	Ship	Station	Method of capture	Depth of water (m)	Lat. (N)	Long. (W)	Date
SIO 68–89	*Thomas Washington*	MV68–I–59	40′ balloon otter trawl	556–635	29°40.2′–29°43.9′	113°55.4′–113°58.0′	1968–I:18
SIO 68–90	*Thomas Washington*	MV68–I–60	40′ balloon otter trawl	545–630	29°39.5′–29°43.5′	113°55.5′–113°59.0′	1968–I:18
SIO 69–203	*Ellen B. Scripps*	MV69–II–6	Free-vehicle trap	746	28°40′	113°53′	1969–III:2
LACM 30063–1	*Velero IV*	11821	Beam trawl	731–1215[4]	28°33.0′–28°46.75′	112°49.5′–113°06.0′	1967–XI:30
LACM 30303–1[2]	*Velero IV*	11837	Beam trawl	1097–1326	28°37.0′–28°40.5′	112°56.0′–113°01.5′	1967–XII:2
LACM 7552 Holotype							
LACM 8818–9 (Paratype)	*Alaska*	64A2–16	Large mid-water trawl	402–412	28°55′	112°50.5′	1964–IV:6
USNM 200413[3] (Paratype)							

[1] LACM = Los Angeles County Museum; SIO = Scripps Institution of Oceanography; USNM = United States National Museum.
[2] The egg case was taken at this station.
[3] This paratype is the only specimen that was not examined or measured by us.
[4] According to the collection records, the beam trawl was calculated from wire angle and ship speed to have fished at the midwater depth of 530–630 fathoms, at least about 100 m off the bottom (see text).

depth of 402–412 m furnished us—and they further stated: "During retrieval, the net actually travelled to the bottom where it rode for sufficient time to pick up several thousand heart urchins . . . mollusks . . . and several kinds of bottom living fishes" (including, in addition to *Galeus: Hydrolagus colliei* (Lay and Bennett), *Coelorhynchus scaphopsis* Gilbert, *Sebastes* spp., *Xeneretmus ritteri* Gilbert, *Symphurus* sp., and others that probably came from the bottom). It therefore seems certain that the trawl did fish on the bottom. Consequently, there is no reason to think that the cat sharks must have been taken above the bottom. One of several large hake, *Merluccius angustimanus* Garman, taken at this station spewed up a partly digested *Galeus.*

The collection records for Velero IV Station 11821, where specimen LACM 30063–1 was taken, indicate, again through measurements of cable angle and ship speed, that the beam trawl was fishing at 530–630 m, or about 100 m or more above the minimum water depth of 731 m. The chief technician therefore thought that there is no reason to believe that the trawl ever hit the bottom. However, such calculation of trawl depth proved erroneous in the station just discussed and we regard it as unreliable, especially where currents and turbulence are so strong. A macrourid recorded as having been caught in the trawl further suggests the probability that the trawl reached the bottom.

We think it highly probable that all the specimens of *Galeus piperatus* have been taken on or very near the bottom.

DESCRIPTION OF EGG-CASE

It has generally been assumed that all scyliorhinid sharks are egg layers, but the discovery that one species, *Galeus polli* Cadenat, gives birth to free-living young (Cadenat 1959) calls for an examination of the mode of reproduction in all the species. (We avoid the terms oviparous, ovoviviparous, and viviparous, since among fishes there is a complete spectrum from the fertilization of eggs some time after deposition to the bearing of virtually mature offspring).

Fortunately we have an egg-case (Fig. 1) that we think almost certainly is that of *G. piperatus*, for the following reasons:

(1) The egg-case was trawled along with an adult of *G. piperatus* in the limited area where this species has been taken.

(2) The minute size of the elongate egg-case is consistent with the dwarf size of the species. Young only 71 and 80 mm long (in preservation) are well formed, and the 80-mm juvenile on being trawled uninjured swam long and very vigorously in a tray of water. The egg-case seems to be of a size adequate to hold a coiled embryo about as long as the smaller free-living juvenile. The three adult males although only 280 to 293 mm in total length have fully elaborated claspers and, therefore, had attained their final size.

Fig. 1. Scyliorhinid egg-case 35 mm long, thought to represent *Galeus piperatus*, taken in trawl with adult male at R/V Velero IV Sta. 11837.

The two largest known females, only 296 and 302 mm in total length, each has "a few large eggs about 7 mm in diameter in the functional right ovary, and are considered sexually mature" (Springer and Wagner, 1966, p. 8). The proportion of the size of the egg-case (35 mm long) to the estimated total length of the mature female is about the same as in other scyliorhinids. The ratio in this species is 118; in *Cephaloscyllium uter* Jordan and Evermann, regarded by Kato, Springer and Wagner (1967) as synonymous with *C. ventriosum* (Garman), 124, on basis of averaging measurements of nine eggs; in *Apristurus brunneus*, 100 (five measurements); in *Schroederichthys maculatus* Springer (data from Springer 1966), 129; in *Galeus melastomus* (data from Tortonese 1956), 112.

(3) The egg-case closely resembles that of *Galeus melastomus* (Rafinesque) as figured by Tortonese (1956) and shows points of resemblance as well as difference when compared with figures of egg-cases referred by Springer (1966) provisionally to *Scyliorhinus meadi* Springer, *S. retifer* (Garman), and *Schroederichthys maculatus* Springer.

(4) The egg-case is surely that of a scyliorhinid and it seems improbable that it pertains to any of the three other species of the family that occur in Golfo de California. Of these, the *Cephaloscyllium* reaches the length of about 1 m and is known to have much larger egg-cases (nine in the Scripps collection average 100 mm in midline length). *Parmaturus xaniurus* attains a length of about 0.5 m, and almost surely has larger egg-cases. *Cephalurus cephalus* (Gilbert) is incompletely known from a few immature specimens (Bigelow and Schroeder 1941) and its egg-case has not been identified.

The tiny, empty egg-case is translucent-brown. It is rather evenly elliptical, and moderately expanded at the truncate anterior end (now slit open), without evident tendrils. The posterior end becomes somewhat thickened as the two closely approximated sides, each ending in the base of a tendril, are arched very closely together. Very fine longitudinal striations parallel the margin.

DESCRIPTION OF JUVENILE

Two juveniles of *Galeus piperatus*, both males, have been collected. The larger (Fig. 2), SIO 68–89, 85 mm in total length in life, 80 mm on preservation, is the one that was noted to swim long and vigorously. The smaller one, SIO 68–90, measures only 71 mm in alcohol, though the yolk-sac is completely absorbed. The larger one was taken with an adult male (SIO 68–89), and both came within the limited area from which adults and the egg-case have been collected.

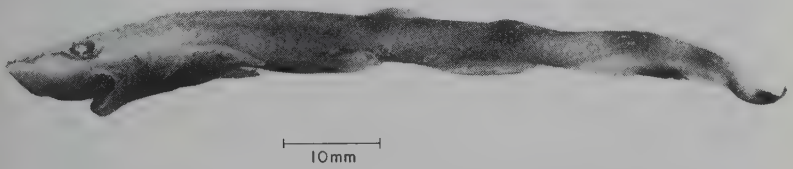

Fig. 2. Juvenile male of *Galeus piperatus*, 80 mm in total length (SIO 68–89).

In coloration the juveniles differ strikingly from the adults. In addition to the large melanophores—the "fine pepper-like spots" (Fig. 3, upper, and Fig. 7) that prompted SPRINGER and WAGNER to name the species *piperatus*—the juveniles bear a series of blackish areas (Fig. 2) formed by the concentration of melanophores. A dark area extends from midsides well onto each dorsal fin. Five distinct dark areas mark the caudal fin. Three are on the upper lobe: one at and below the upper caudal origin, another midway along the dorsal lobe, and an intense black area on the upper part of the caudal tip, leaving the extreme end of the caudal axis unpigmented. The ventral lobe bears two dark blotches, one at the extreme end and one below the pale area between the first two upper spots. This color pattern is similar to that figured for juveniles of *Galeus polli* CADENAT (1959, Fig. 17), and seems to homologize with the dark saddles and caudal blotches described and figured by SPRINGER (1966) for the adults of several species referred to *Scyliorhinus*, *Galeus* and *Halaelurus*.

In life, the larger juvenile was pale purplish-brown on the upper and posterior parts and silvery on the belly. The dusky to black markings were very conspicuous, and the extreme tip of the caudal lobe was milky white.

The inside of the mouth is not as intensely dark as in adults. The melanophores are limited to the posterior half of the roof of the buccal cavity and the anterior half is quite pale. No denticles are borne in this region in juveniles, but the anterior section bears numerous fleshy tubercles about as large as the teeth. These appear to be sensory papillae, which in the adult are retained, though obscured by the denticles that largely cover this region (as noted below).

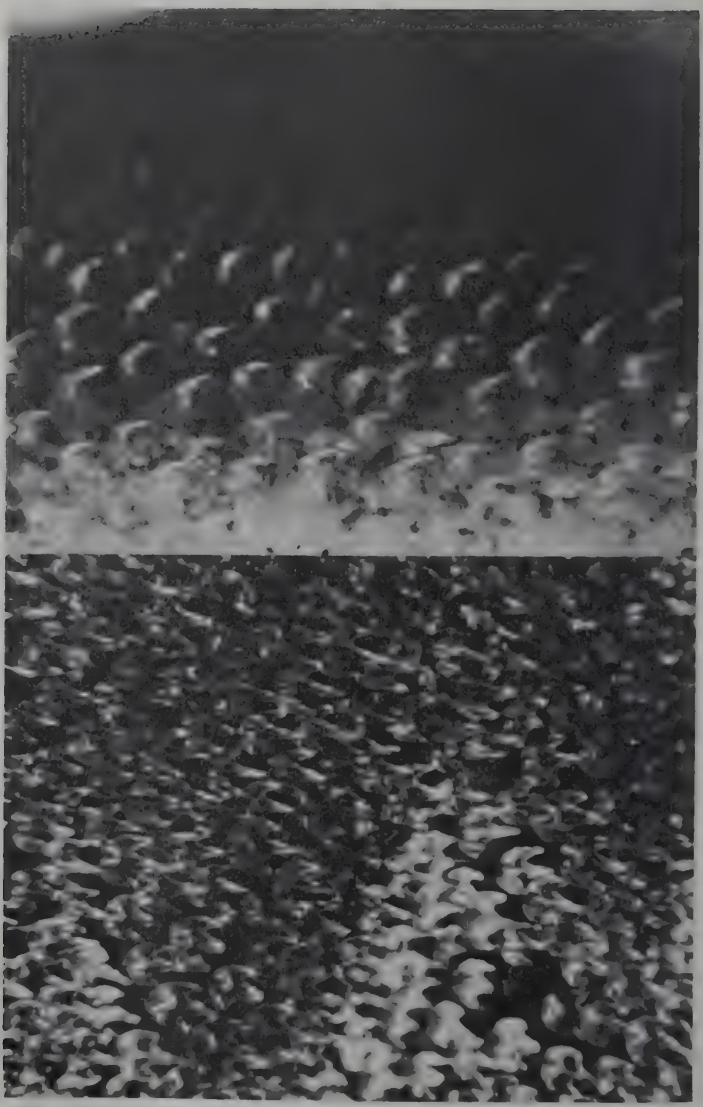

Fig. 3. Denticles of *Galeus piperatus*. Above: denticles of SIO 68–89, an 80-mm juvenile male. Below: denticles of SIO 68–89, a 284-mm adult male. Both views are of areas below the first dorsal fin and are magnified about 70 × (anterior to the left).

The denticles on the body (Fig. 3) of the juveniles differ notably from those of the adult. Instead of being trident-shaped and bearing a high central ridge and a less elevated marginal ridge above and below, the denticles on the juveniles are long, hooked spines with only the median element apparent. Instead of being borne on a pedicel, they are sessile. The specialized denticles that form the crest on the caudal fin—a feature of the genus *Galeus*—resemble those of the adult.

The teeth of the juveniles, both males, resemble those of the adult males (as described below). The lower jaw bears a total of only ten to thirty irregularly arranged teeth. At the lip line there is a definite transition between the teeth and the denticles.

The vertebrae are apparently completely formed in this species by the time a length of 70–80 mm has been attained, for the numbers in young and adult are approximately equal (Table 3), even in the caudal region, with the possible exception of one or a very few terminal rudiments, because they are not all completely calcified. Thus, the early development of adult characters in this dwarf species is highlighted. The contrast in relative lengths of monospondylous and diplospondylous vertebrae seems greater in the juveniles than the adults, but the penultimate monospondylous vertebra is much less elongate in form in the juvenile than in the adult, yielding a lower "B" ratio (Table 3). However, as noted below, this ratio is of somewhat dubious significance.

Although essentially adult form is attained at an exceptionally small size, the juveniles differ from adults in various morphometric features (Table 2). As is usual in elasmobranch development the urosome is markedly elongated in juveniles, as is shown by measurements 5, 6, 10, and 56, most notably for the caudal-fin dimensions (44, 45). In compensation, the predorsal lengths (1, 2) are shorter. The relative shortening of the anterior regions involves primarily the anterior trunk (the measurement from insertion of pectoral fin to origin of first dorsal, 7, constitutes 16 or 17 instead of 19 to 25 per cent of the total length). Measurements involving the head do not change markedly. Oddly, the orbit-length proportion (30) remains essentially constant. The caudal peduncle (14, 16) is proportionately deeper and wider in the juveniles. The vertical fins have longer bases (39, 42, 45, 55), and, correlatively, interdorsal space (4) is shorter. The paired fins (46–52) are much smaller. The gill-slits (18) are more closely approximated ventrally, but the interorbital width and interspiracular distance (31, 32) seem to be somewhat greater. In certain changes with age, especially the elongation in the dimensions of the snout (19–22, 34), the shortening of the mouth-projection measurement (28), and the broadening of the mouth (29), the abrupt transformation apparently occurs over the size range of our two young specimens (71 to 80 mm in total length).

MORPHOMETRY

All known specimens of the species, with the exception of the two mislaid individuals that were trawled with the types and of one paratype (USNM 200413), have been measured for fifty-seven dimensions (Table 3). This has been done to illustrate morphometric differences between juveniles and adults, as just indicated and to determine what differences, if any, distinguish the sexes. These measurements, furthermore, provide data for future comparisons of *G. piperatus* with other species, particularly with the western North Atlantic cognates, *G. arae* (Nichols) and *G. cadenati* Springer (1966), and with the three species described from eastern Asia: *G. eastmani* (Jordan and Snyder) from Japan, *G. sauteri* (Jordan and Richardson) from Taiwan, and *G. hertwigi* (Engelhardt) from Japan (references in Springer and Wagner 1966).

For greater accuracy measurements were taken from point to point. The only projection measurement was "mouth length" (Number 28 in Table 2). Precision dial calipers were used on the larger specimens, under magnification as needed. The two juveniles were measured with an optical micrometer. Origins of vertical fins and insertions of paired fins were located by gently pushing one point of the calipers against the anterior base of the fin until slight resistance was felt. Depending on obvious context, either the minimal or the maximal measurement was employed. In general, the methods follow the recommendations of Hubbs and Lagler (1964), and, with some exceptions and additions, are those used in Hubbs, Iwai and Matsubara (1967) in describing another dwarf shark. The method of measurement was somewhat modified for several parts, numbered as in Table 2:

2, "Length to D2", and all other dimensions, were measured linearly and none were computed by addition.

10, "D2 origin to upper C origin", and all other measurements involving the upper lobe of the caudal fin, were made considering the upper caudal origin to occur at the extreme front of the row of modified denticles cresting the caudal fin (Fig. 5).

13, "Body depth (greatest)" and 15, "Body width (greatest)", and other dimensions were measured as the specimen, if distorted by preservation, was manipulated to approximate its normal form in life.

20, "Snout length (preoral)", was taken by us from tip of snout to the margin of the lip on the midline.

21, "Prenarial length, outer" represents distance from tip of snout to nearest point of margin of outer opening of nostril.

22, "Prenarial length, inner" represents distance from tip of snout to extreme inner-posterior angle of nostril.

28, "Mouth length (projection)" was measured from margin of upper lip along a mid-sagittal line to a straightedge laid between extreme ends of gape.

29, "Mouth width" is the distance between extreme corners of the gape.
44, "Upper lobe C (extreme)" and 45, "Lower lobe C (extreme)" are measured between the appropriate origin and the extreme tip of the caudal fin.

All measurements are expressed as thousandths of the standard length. The abbreviations used for fins are: P1 = pectoral, P2 = pelvic, D1 = first dorsal, D2 = second dorsal, and C = caudal.

Comparison of the measurements of three adults of each sex (Table 2) disclosed hardly a trace of sexual dimorphism. The length of the abdomen, as measured between the insertions of the paired fins (dimension No. 12) averages slightly higher in females (189) than in males (178), but the difference is much less notable than was indicated for the pelagic dwarf shark *Euprotomicrus bispinatus* by Hubbs, Iwai and Matsubara (1967, pp. 13–14, Fig. 1). In that form the greater length of the abdomen in females was suggested "as an adaptation to fecundity in a dwarfed shark". The difference may be related to the simultaneous development of the whole brood by *Euprotomicrus bispinatus* and the presumable development of mature eggs one by one in *Galeus piperatus*.

COLOR

In the original description of *Galeus piperatus* stress was placed on the uniformity of the coloration, with the exception of the sprinkling of large melanophores (such as shown in Figs. 3, upper, and 7) in the largest known specimen, the holotype (LACM 7552, 302 mm in total length). The somewhat smaller paratypes were described as having "irregular and indistinct blotches that contrast little with the background color". Our subsequently collected specimens show moderately conspicuous dark markings set off by a narrow, light, subhexagonal reticulum, approaching that figured by Springer (1966, Fig. 20) for a specimen of *G. arae* (Nichols) of comparable size. The figure of the holotype and the specimen itself show almost no trace of a blackish margin along the anal and caudal fins and little blackening on the dorsal fins, but our specimens show these markings strongly. We suspect that the lack of contrast in the types is attributable at least in part to the method of preservation.

Life colors were recorded on a 280-mm fully adult male (SIO 68–89–5A1). Dorsally the color is rather rich brown. The ventral region of the trunk is gray, with bright-blue reflections. A wide dorsolateral stripe, extending to between the dorsal fins, is marked by a pale subhexagonal network colored like the belly. In contradistinction to the original description, there is a sharp contrast between the dorsal and ventral color. A mid-dorsal stripe is slightly lighter and yellower than the reticulum. There is an irregular trace of the reticulations on the tail.

Table 2. Measurements of *Galeus piperatus* in thousandths of total length.

Specimen no.	Male					Female		
	SIO 68–90	SIO 68–89	SIO 69–203	SIO 68–89	LACM 30303–1	LACM 8818–9[2]	LACM 30063–1	LACM 7552[1]
Total length (mm)	71	80	280	284	293	256	295	302
1. Length to D1	427	417	464	451	451	430	468	440
2. Length to D2	592	569	621	623	608	598	624	613
3. Between dorsal origins	159	152	161	165	163	157	158	171
4. Interdorsal space	75	62	88	89	87	81	85	88
5. D2 origin to end C	408	435	379	380	403	406	369	383
6. Tip D2 to end C	335	352	305	301	318	329	302	308
7. P1 insertion to D1 origin	170	160	208	194	226	209	251	200
8. Prepectoral length	211	227	238	224	223	219	234	195
9. Prepelvic length	390	373	386	391	375	363	393	358
10. D2 origin to upper C origin	111	130	98	89	92	107	96	99
11. P2 insertion to lower C origin	255	227	225	244	232	238	214	262
12. Between P1 and P2 insertions	182	176	186	177	171	200	192	176
13. Body depth (greatest)	82	77	99	103	100	73	94	115
14. C peduncle depth (least)	44	40	39	39	38	36	38	36
15. Body width (greatest)	89	95	93	89	89	100	87	86
16. C peduncle width at front C	23	22	20	18	19	16	21	16
17. Length to first gill-slit	177	181	188	175	183	174	201	163
18. Width between first gill-slits (ventrally)	80	97	111	97	110	101	104	108
19. Snout length (preocular)	82	91	85	83	83	88	86	77
20. Snout length (preoral)	58	79	80	72	76	80	86	70
21. Prenarial length, outer	49	53	55	55	52	55	57	51
22. Prenarial length, inner	51	68	64	61	61	59	63	56
23. Nostril width (maximum)	26	30	25	25	26	25	29	26

Specimen uo.	Male					Female		
	SIO 68–90	SIO 68–89	SIO 69–203	SIO 68–89	LACM 30303–1	LACM 8818–9[2]	LACM 30063–1	LACM 7552[1]
24. Internarial width (least)	29	31	27	28	27	27	28	27
25. Between tips of narial flaps	57	55	56	54	62	62	58	61
26. Nostril to orbit (least)	29	34	34	29	30	24	35	27
27. Nostril to mouth (least)	16	17	18	19	18	21	25	20
28. Mouth length (projection)	64	58	49	43	43	36	41	37
29. Mouth width	85	90	108	100	103	132	104	95
30. Orbit length	41	42	39	43	41	41	42	40
31. Interorbital width (fleshy)	89	110	86	85	84	82	87	86
32. Interspiracular distance (dorsally)	107	109	105	95	100	101	106	96
33. Spiracle length (maximum)	9	10	6	5	9	10	4	7
34. Spiracle to snout tip	134	148	137	132	131	128	138	127
35. Spiracle to P1 insertion	138	146	159	150	151	153	159	141
36. Between fronts of gill-slits 1 and 5	60	70	49	55	60	67	49	61
37. Height, first gill-slit	28	21	21	26	26	19	20	20
38. Height, fifth gill-slit	19	13	13	19	17	11	13	15
39. D1 base	54	57	45	45	43	50	50	49
40. D1, origin to extreme tip	89	97	75	76	76	88	84	78
41. D1 height (insertion to extreme tip)	36	39	38	39	45	49	42	32
42. D2 base	58	57	49	43	47	48	47	49
43. D2, origin to extreme tip	87	95	74	68	74	75	72	71
44. Upper lobe C (extreme)	314	322	281	286	307	292	278	284
45. Lower lobe C (extreme)	325	362	289	290	319	311	287	303
46. P1 base (fin appressed)	41	49	70	69	67	67	77	67
47. P1, lower-anterior edge	85	110	121	128	120	127	119	117
48. P1, lower-distal edge	44	47	103	86	90	95	91	101

Specimen no.	Male					Female		
	SIO 68–90	SIO 68–89	SIO 69–203	SIO 68–89	LACM 30303–1	LACM 8818–9[2]	LACM 30063–1	LACM 7552[1]
49. P2 base	60	70	84	77	74	76	100	79
50. P2 origin to tip of rays	74	99	118	101	99	116	116	113
51. P2 origin to tip clasper	64	78	162	159	157	—	—	—
52. Cloaca to tip clasper	31	35	107	105	102	—	—	—
53. Cloaca to tip P2 rays	42	69	70	52	52	74	71	65
54. Snout to anal-fin origin	514	492	561	553	533	504	536	540
55. Length anal base	132	125	112	108	122	128	134	123
56. End of anal fin to lower C origin	35	16	14	20	9	14	11	12
57. Length anal fin	141	151	127	129	140	146	146	146

[1] Holotype.
[2] Paratype.

DENTICLES

To supplement the original account of denticles on the body of adults we include (Fig. 3, lower) the reproduction of a photomicrograph of the pedunculated tridents, which contrast boldly with the simple, hooked, sessile spinelets of the juveniles (Fig. 3, upper), as already noted. The denticles on the body also contrast sharply with the minute lanceolate oral denticles noted and figured by Springer and Wagner (1966, pp. 3–4, Fig. 2) for *G. piperatus* and found by them in all species of *Galeus* that they examined. The occurrence, distribution, and form of denticles on the surfaces of the buccal cavity provide diagnostic characters in sharks, as the late Swiss paleontologist Bernhard Peyer found during unpublished research at Scripps Institution several years ago.

The specialized form and pattern of the denticles on the clasper are mentioned below.

TEETH

The collection of males makes it possible to point out sexual dimorphism in the tooth structure of adults, somewhat in the direction of, but far less extreme than, the sexual dimorphism of the teeth in *Apristurus riveri* Bigelow and Schroeder, as described and figured by Springer (1966, pp. 591–593, Fig. 10). The females exhibit a greater degree of heterodonty than the males. The teeth of females vary from tricuspid anteriorly, with a long central cusp near the symphysis, to posterior teeth with cusps, of more uniform length, numbering four or five in the upper jaw and five to seven in the lower jaw (Fig. 4). In males, tricuspid teeth continue to the end of the jaw, with some reduction in relative length of the central cusp. One male (SIO 69–203) bore a few pentacuspid teeth near the end in each jaw. Generally, all teeth of the adult males are similar to the anterior tricuspids of the females. As already noted, small juvenile males have teeth similar to those of adult males.

In adults of each sex the tooth rows range from twenty-nine to thirty-two on each side of the jaw.

VERTEBRAE

As determined by radiography, the vertebrae in eight specimens vary in number as follows (Table 3): monospondylous vertebrae 30 to 33 (mean 32.7), precaudal diplospondylous vertebrae 36 to 39 (37.4), total precaudals 66 to 72 (69.1), caudals 41 to 49 (45.6), total count 112 to 118 (114.7). In all the radiographs the monospondylous vertebrae give way to the diplospondylous condition clearly and abruptly over the insertion

Fig. 4. Teeth from the left jaw of an adult female of *Galeus piperatus* (LACM 8818–9, a paratype, 256 mm long). Upper jaw, above; lower jaw, below. The first figure represents the number of teeth between that tooth and the symphysis; the second figure, the number of teeth between that tooth and the end of the jaw.

of the pelvic fins (Fig. 5), thus rendering precise the counting of monospondylous centra. The diplospondylous vertebrae are designated as precaudal and caudal, by the definition of the first caudal (Fig. 6) as the first vertebra lying wholly or by any part below the beginning of the double row of tubercles that dorsally crest the caudal fin (the same point that is regarded by us, for measurements, as the origin of the caudal fin).

The very early virtual completion of vertebral formation reflects the dwarfed nature of the species, as already noted in discussing the juveniles.

Our counts of the holotype and one paratype show some divergence from those by Springer and Wagner (1966). The counts of monospondylous vertebrae agree, but the diplospondylous precaudal counts (obtained by subtraction from their Table 3) differ by as much as three and the caudal counts by as much as five. Perhaps those workers chose a different point for the caudal origin, or counted caudal rudiments differently. In his review of western Atlantic scyliorhinids Springer (1966) presented counts of monospondylous vertebrae only, stating that "diplospondylous vertebrae near the tail tips were difficult to count". Whereas monospondylous and precaudal diplospondylous counts are quite precise, the number of caudal vertebrae is subject to some counting error due to

Table 3. Vertebral characters in eight specimens of *Galeus piperatus*, from radiographs.

Specimen no.	Sex	T. L. (mm)	Precaudal vertebrae		Total precaudal vertebrae	Caudal vert.	Total vert.	A[1]	B[2]
			Mono-spondylous	Diplo-spondylous					
SIO 68–89	♂	284	31	39	70	46	116	146	130
SIO 68–89	♂	80	31	38	69	45	114	188	93
SIO 68–90	♂	71	33	39	72	41	113	186	85
SIO 69–203	♂	280	33	36	69	47	116	143	142
LACM 30303–1	♂	293	30	36	66	47	113	149	142
LACM 7552 (Holotype)	♀	302	33	36	69	49	118	136	127
LACM 8818–9 (Paratype)	♀	256	31	39	70	46	116	178	124
LACM 30063–1	♀	295	32	36	68	44	112	156	140
Averages			32.7	37.4	69.1	45.6	114.7	160.3	122.9

[1] $A = \frac{\text{length of penultimate monospondylous centrum}}{\text{length of first diplospondylous centrum}} \times 100.$

[2] $B = \frac{\text{length of penultimate monospondylous centrum}}{\text{diameter of penultimate monospondylous centrum}} \times 100.$

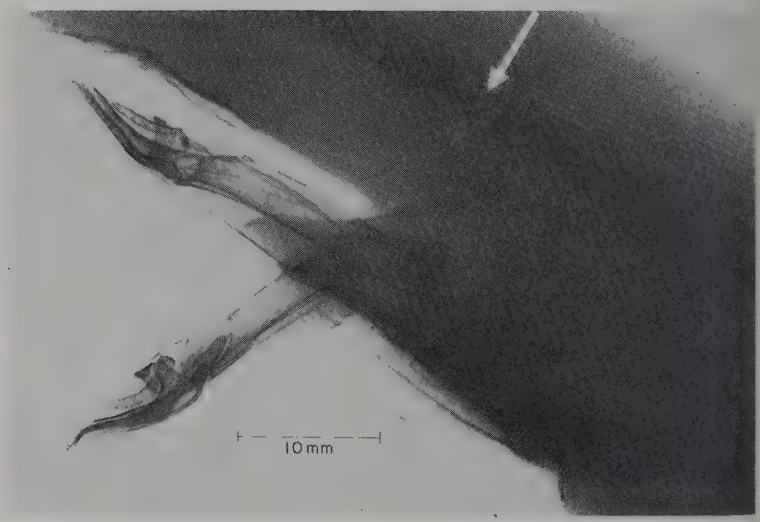

Fig. 5. Radiograph of pelvic claspers and median vertebrae of adult male *Galeus piperatus* in right lateral view (SIO 68 89). Arrow indicates point of change from monospondyly to diplospondyly.

Fig. 6. Radiograph of caudal fin of holotype of *Galeus piperatus*. Arrow indicates beginning of double row of enlarged denticles used as a marker for origin of caudal fin and caudal vertebrae.

the minute and irregular size of the centra and the distorted shape of the last few elements. Nevertheless, we feel that with good X-ray equipment, and with due care in exposures and in counting, that reasonably reliable counts can be obtained for the diplospondylous vertebrae—certainly for the precaudal ones, if a precise point for the start of the precaudal count is established.

Other striking differences occur between our values and those of Springer and Wagner (1966) for the "A" and "B" ratios (defined in Table 3), which were originally proposed and utilized by Springer and Garrick (1964). Furthermore, the range of variation for each ratio is very large. In small sharks, such as *Galeus piperatus*, a typical vertebra is about 2–3 mm long. Measurement under magnification is essential, but is complicated by the large grain size that appears under such enlargement. The limits of the centra are difficult to ascertain with certainty. In addition, different exposure times can cause measurements for the same specimen to diverge. This results from the circumstance that inadequate X-ray exposures fail to represent the full length of the centra, because the thin fore and aft ends of the amphicoelous vertebrae fail to register, whereas the width of the centrum remains scarcely altered. Until exposure times and methods of measuring can be standardized, we feel that the "A" and "B" ratios will be of little value, especially for small sharks.

CLASPERS

The claspers of *Galeus piperatus* (Fig. 7) are large, robust, and highly complex, particularly as shown by radiography (Fig. 5). They are very mobile and are jointed about midway of their length. The siphons open laterally at about 0.9 of the distance out from the cloaca. The pattern of grooves and of hard and soft flaps, folds, and prominences is complicated but consistent. The detailed structures and homologies are yet to be worked out, and we are pleased to learn that Stewart Springer has undertaken a study of the claspers of the Scyliorhinidae. In gross features, the clasper of *G. piperatus* conforms with Springer's (1966, Fig. 4B) sketch of the claspers and general pelvic region in a western North Atlantic species, *G. arae* (Nichols), and definitely contrasts with Leigh-Sharpe's (1920) non-detailed brief account and figures for the European species *Scyllium catulus* = *Scyliorhinus catulus* (L.) and *Scyllium canicula* = *Scyliorhinus canicula* (L.). We feel that in all probability the finer structure of the diverse elements of the clasper will provide key value in the recognition of genera and species of Scyliorhinidae and in the interpretation of their relationships.

The denticles on the clasper are distinctively modified in pattern and

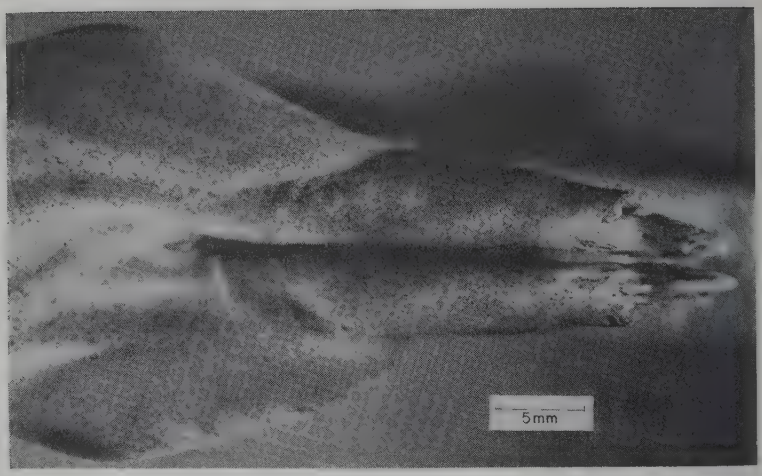

Fig. 7. Pelvic claspers of adult male of *Galeus piperatus* (SIO 68–89).

form. They completely cover a large area over the ventral surface basally. Distally, this area spirals laterally and dorsally. This major patch is continuous with the squamation of the flat lower surface of the pelvic fins, though the intervening denticles are weak. The patch ends abruptly against the smooth denticle-free skin, which is irregularly marked with black (Fig. 7). Beyond the subterminal notch in the clasper as seen in ventral view (Fig. 7), and just proximal to the whitish flesh-covered tip of the clasper, there is a discrete patch of denticles, which are mostly loose and lanceolate, but outward and upward, where concealed by a prepuce-like hood, they become strong and fixed. On the opposite side, opposite the basal part of the terminal patch and extending farther proximally, is a second discrete patch of denticles, which are moderately flattened, slender and sharply pointed.

Most notable among the diverse denticles on the clasper are the very slender, mostly loosely attached hooks that biserially line the edge of the spiralling sperm duct on the outer and upper sides of the organ. A few occur at the outer tip of the subterminal notch as seen in ventral view (Fig. 7), but the main part of the double file is along the firm edge that angles proximad and entad. The hooks arise from a dorsal terminal cartilage (Fig. 6). These hooks closely approach the denticles on the body of the juveniles (Fig. 3, upper).

An example of the finding of profound differences in clasper characters between two species of squaloid sharks that were long thought, probably

erroneously, to be very closely related, has recently been presented (Hubbs, Iwai and Matsubara, 1967, pp. 33–36, Fig. 7, pls. 2, 6, 7). Thorough critical, detailed, and comparative studies of myxopterygial structures in all sharks are, indeed, long overdue.

SUMMARY

Information is presented on a recently described dwarf shark, *Galeus piperatus*, which occurs through a wide range of depth in turbulent waters of highly varying physical parameters in Golfo de California, Mexico. It barely exceeds 300 mm in total length and an egg-case presumed to be of this species is only 35 mm long. Young about 80 mm long are well formed and very active. The sexes are remarkably alike in most respects but differ in tooth structure. The denticles of the young bear a single hooked spine, but are pedunculated tridents in the adult. The claspers are large, robust, and of highly complex external and internal structure.

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ON THE MIGRATIONS OF THE COD IN THE SKAGERAK SHOWN BY TAGGING EXPERIMENTS IN THE PERIOD 1954—1965

By

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INTRODUCTION

Tagging experiments on cod carried out in the skerries and fjords on the Norwegian Skagerak coast have shown that the cod population or populations in the area undertake only short migrations and are more or less isolated from the cod in other areas of the Skagerak (Dahl 1906, Ruud 1939, Løversen 1946). Two tagging experiments conducted from the Biological Station in Flødevigen in 1953 and 1954 showed, however, that cod from the Skagerak coast could undertake longer migrations along the Norwegian coast as well as into the Skagerak (unpublished data). These contradictory results, as compared with previous years tagging experiments, inspired the former director, Dr. A. Dannevig, to initiate tagging experiments also from the Danish side of the Skagerak. This paper describes the results of eleven tagging experiments carried out in the years 1954 to 1965.

MATERIAL AND METHODS

The tagging experiments were carried out in the years 1954, 1955, 1956, 1958, 1960, 1961 and 1965 during cruises with R/V G. M. Dannevig. The cod used for tagging were caught with hand line, and only fish in good condition were tagged. In all the years the fish were released at Robben (N 57°42′, E 09°12′) about 25 n.m. from the Danish Jylland coast. In 1954 and 1958 tagged fish were also released at Rubjerg (N 57°30′, E 09°35′), and in 1956 near Hanstholm (N 57°15′, E 08°00′).

The Lea hydrostatic tag was used in all the experiments except in one experiment in 1954 when a tag consisting of impregnated paper printed

Contribution given in honour of Gunnar Rollefsen at his 70th birthday.

with necessary text, and rolled together to about the same size as the Lea tag was used.

All the tags were fixed in front of the first dorsal fin with a nylon thread.

The total length of the tagged fish ranged from 22 to 110 cm with a mean length of 56 cm, and the greatest frequencies were in the size groups 41 to 70 cm.

The number of tagged fish each year varied from 87 in 1956 to 309 in 1960, totalling 1,244 fish. The number of tagged fish and recaptures are given in Table 1.

RESULTS AND DISCUSSION

Of the 1,244 tagged fish a total of 367 or 29.5% had been recaptured within the end of May 1969. Tags (14) which have been reported found on the shore along the Danish, Norwegian and Swedish coast are not included in this figure. Of 44 fish tagged in 1954 with the impregnated paper tag, 11 fish have been recaptured compared to 12 recaptures of 45 fish tagged at the same locality and the same year with the Lea tag. The two tags are therefore treated in the present report as having the same tagging efficiency.

The recapture percentage from the different tagging years shows a variation from 24.9 to 35.6. The number of recaptures decreased rapidly after the first year in liberty (Table 1). The two experiments in 1954 gave no recaptures in the third year, and in general the number of recaptures in the third year was very small. The longest time in liberty was 83 months. In the total material the mean number of months before reapture is about the same in the different length groups.

The total material shows that the recapture percentage was higher in the larger length groups than in the smaller ones. Of 110 tagged fish in the group 41–45 cm 14.6% were recaptured compared to 43.2% recaptured from the group 66–70 cm with 111 fish (Fig. 1). This could either be due to availability, mortality, a higher shedding percentage among the smaller fish, or a combination of these factors. Lefranc (1967) also got fewer recaptures from the smaller cod and assumes that the mortality could be higher among the smaller ones. The same decreasing recapture tendency with decreasing size at tagging was also shown on whiting by Knudsen (1964).

All the recaptures in the Skagerak have been taken on the Danish side of the Norwegian Channel. No fish from any of the three tagging localities was recaptured on the Norwegian Skagerak coast though the nearest tagging position, Robben, is only about 40 n.m. from the coast. Tagging experiments in the skerries on the Norwegian Skagerak coast in the years

Table 1. Number of cod tagged and recaptured in the years after tagging, and the percent returns from the different tagging years.

Date	Locality	Number of cod tagged	Years at sea							Sum recaptured	Total % returns tagged in the different years
			1	2	3	4	5	6	7		
1954 Aug.	Robben	64	8	4						23	25.8
1954 Aug.	Rubjerg	25	10	1							
1955 April	Robben	129	22	7	6	5	2	1	1	44	34.1
1956 April	Robben	49	11	2	1				1	31	35.6
1956 April	Hanstholm	38	7	6	2		1				
1958 Aug. Sept.	Robben	110	20	2	2						
1958 Aug. Sept.	Rubjerg	104	26	10	2	2	2			101	34.1
1958 Nov.	Robben	82	22	10	3						
1960 May	Robben	188	33	16	9		2			83	26.9
1960 Aug.	Robben	121	16	4	1	1	1				
1961 Aug.	Robben	195	31	13		1		1		57	24.9
1961 Nov.	Robben	34	6	3	1	1					
1965 March	Robben	105	17	9	1		1			28	26.7
Total		1244	229	87	28	10	9	2	2	367	29.5

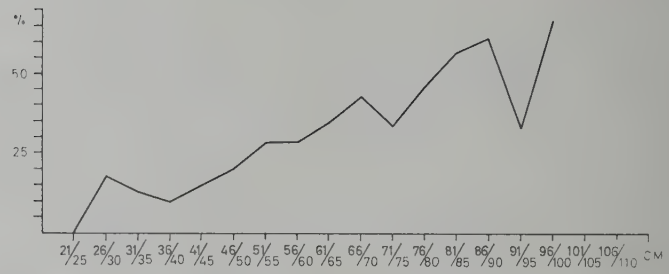

Fig. 1. Percent recaptured cod according to length when tagged. (Number of tagged fish in each of the 5-cm groups: 33, 47, 42, 110, 148, 140, 211, 225, 111, 62, 52, 30, 18, 3, 3.)

1953 and 1954 gave some returns from the Danish side of Skagerak (unpublished data). As the fish in these experiments had been kept in a spawning basin at Flødevigen for some weeks before tagging, the long migration may, however, have been an effect of the captivity. It seems reasonable to conclude therefore, that there usually is no connection between the cod populations on the Danish and the Norwegian Skagerak coast.

Most of the recaptures are taken near the tagging localities. From the Robben experiments 25.6% have been caught within 10 n.m. of the Danish coast, mostly from October to December (Fig. 2). No one was taken near the coast in July, only one in August and one in September. Farther off the coast most of the fish were taken from July to September. Dannevig (1966) mentions that the cod on the Norwegian Skagerak coast migrate to deeper water in the summer due to the warm surface water and return to shallow water in the autumn. A similar seasonal variation in recaptures is also shown in this material and could possibly be due to migration to deeper water in the last part of the summer and early autumn, and to shallow water in the late autumn.

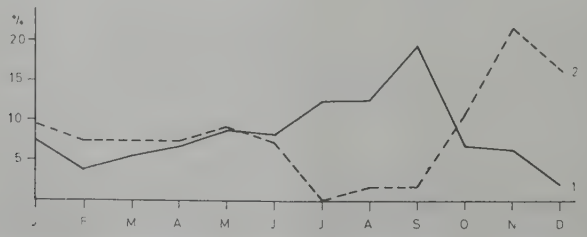

Fig. 2. Monthly variations in the recaptures in the Skagerak. 1) outside and 2) inside a limit of 10 n.m. off the Danish coast.

From the Hanstholm experiments one cod has been recaptured near Robben and four near Hanstholm on the Danish coast. Five have been caught in the eastern part of the North Sea and four near the tagging position.

Table 2. Total number of recaptures in Skagerak, the North Sea and Kattegat from each tagging year (Hanstholm experiment excluded).

Year	Skagerak	North Sea	Kattegat	Total
1954	18	2	2	22
1955	34	7	1	42
1956	10	5	0	15
1958	83	5	6	94
1960	58	10	3	71
1961	37	9	3	49
1965	19	5	0	24
Total	259 (81.4%)	43 (13.6%)	15 (4.7%)	317

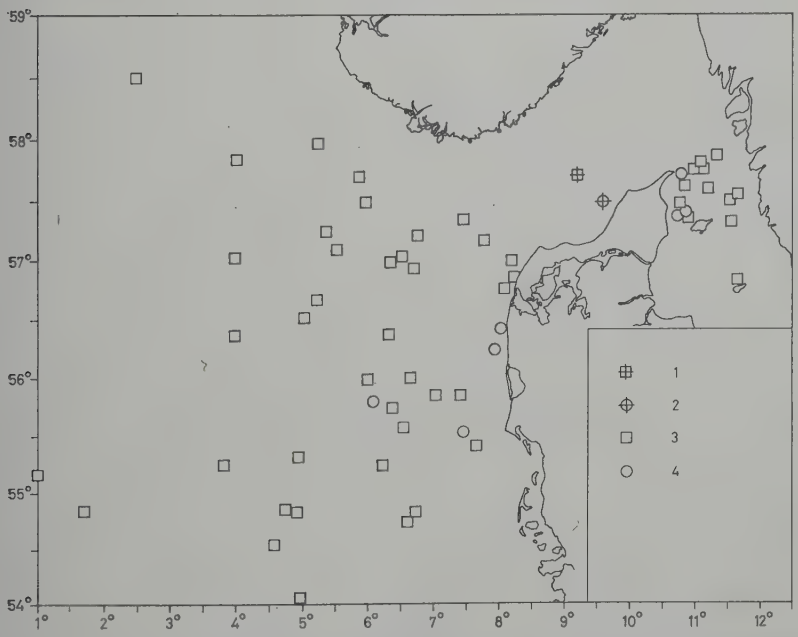

Fig. 3. Recaptures from the North Sea and Kattegat. Tagging positions. 1) Robben and 2) Rubjerg. Recaptures from 3) Robben and 4) Rubjerg.

As shown in Table 2 only 4.7% of the recaptures are from Kattegat (the border between Skagerak and Kattegat defined by a straight line from Skagen to Paternoster Lighthouse), and they have all, except one recaptured near Anholt, been taken in the area between Læsø and the border to Skagerak (Fig. 3). With two exceptions they have all been caught in the period from November to February.

From the Robben and Rubjerg experiments 13.6% of the recaptures have been caught in the North Sea, which should indicate a connection between the cod in the Skagerak and the eastern part of the North Sea. As Fig. 3 shows, all the cod except three are taken east of E 03°50′ and between N 54°00′ and N 58°00′ with a random distribution in the area. Most of them have been taken in the first months of the year. In the southern and middle part of the area, south of N 57°00′, most of the cod were caught during the first six months of the year, mainly from February to April (Table 3). Only three individuals have been taken from July to December. According to Bedford (1966) the central North Sea cod have in the summer (May to September) a northerly movement. Although the number of recaptures from the North Sea in the present material are few, the numbers are higher from the northern part (north of N 57°00′) than from the southern part in this period.

Two fish from these tagging experiments made very long migrations. One cod, 72 cm long, was tagged on Robben in March 1965 and recaptured 49 months later on the Norwegian Helgeland coast. It is interesting to note that Hylen (1964) reported a similar migration, but in opposite direction of a cod tagged on the Trøndelag coast and recaptured west of Skagen. The longest migration was made by a fish tagged on Robben in May 1960 and recaptured 34 months later on the Fyllas Bank on West Greenland. The shortest possible distance between the two places is 2,300 nautical miles. The total length of the fish was 65 cm at tagging and 93 cm when recaptured. A similar long journey, from the North Sea to the Grand Banks, has earlier been reported by Gulland and Williamson (1962). Long migrations of cod have also been observed in other areas, as for example between Iceland and Greenland, from Iceland to the Faeroes and from the Faeroes to the North Sea (Tåning 1934).

Table 3. Number of cod recaptured in the North Sea in the different months.

	Jan.	Feb.	Mar.	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
North of 57°N	1	1		1	1		1	5	1	2		
South of 57°N	3	7	7	5	3	2	2					1

SUMMARY

1. A total of 1,244 cod was tagged from 1954 to 1965. The recapture percentage from the different tagging years varied between 24.9 and 35.6 with a mean of 29.5 for the whole period.

2. No cod has been recaptured on the Norwegian Skagerak coast, indicating that there is no connection between the cod populations on the Danish and Norwegian side of the Skagerak.

3. The recaptures in the Kattegat have been very small (15 individuals). The migration into the eastern part of the North Sea somewhat greater (43 individuals), and they were mainly caught in the first part of the year.

4. One cod has been recaptured on the Fyllas Bank on the West Greenland 34 months after the tagging, and one on the Norwegian Helgeland coast after 49 months at sea.

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PREDICTED EFFECTS OF FERTILIZERS UPON THE ALGAE PRODUCTION IN FERN LAKE[1]

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INTRODUCTION

Fern Lake is situated about 60 km south-west of Seattle in Kitsap County, Washington, U.S.A. (Fig. 1). The lake was, in 1958, made the object of a 10-year research project by the Laboratory of Radiation Biology, University of Washington, with the Washington State Department of Game and the U.S. Atomic Energy Commission as sponsors. The objective was to study the mineral metabolism in the entire watershed in an attempt to accumulate knowledge for the improvement of natural resources (Donaldson, Olson and Donaldson 1959).

Limnological descriptions of the lake are given by Geldiay, Donaldson and Olson (1959) and by Olsen and Olson (1966). Details of the metabolism of certain elements have been gathered through tracing radioactive isotopes such as P-32, Ca-45, I-131 and Mo-99, using the whole lake as experimental field (Donaldson 1962), (Donaldson 1964), (Palumbo *et al.* 1963).

The lake has been extensively studied both with respect to the rate of gross production by phytoplankton, composition and quantities of zooplankton and insects, as well as the growth of the fish. Originally the fish population consisted of eight species. To simplify the whole ecosystem to better control the fish production, the lake was depopulated in 1957 and again in 1960. Restocking has annually been made with 7,000–20,000 steelhead broods (*Salmo gairdneri*). The production of the lake is low, for fish in the order of 1/10 of the nearby Bay Lake, which has been used for comparison. Olsen, Chakravarti and Olson

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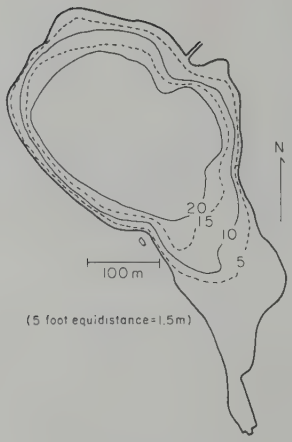
Contribution given in honour of Gunnar Rollefsen at his 70th birthday.



Height above sea level	Appr. 64 m
Area of watershed incl lake	Appr. 800 ha
Area of lake	9.65 ha
Depth, max.	7.6 m
Depth, mean	4.3 m
Volume	416,170 m^3
Length	625 m
Breadth, mean	154 m
Shoreline	1683 m
Development of shoreline	1.5
Development of volume	1.7
Variation of water level	±0.3 m

Fig. 1. Fern Lake. Morphometric data (Olsen and Olson 1966).

(1967) analyzed the spectrum of macro- and micro-element composition of the water, and demonstrated extremely low levels for most of the plant nutrients. They concluded that a nutrient deficiency was seriously limiting the production of the lake. By comparing the mineral composition of Fern Lake with that of the productive Bay Lake it seemed reasonable that the productivity of Fern Lake could be improved by fertilizing the water with the whole spectrum of elements, bringing them to the levels of Bay Lake. On the basis of such evaluations, Olsen (1965) suggested the composition and amounts of fertilizers to be used (Table I).

Before the fertilization of the lake was initiated, pilot experiments were carried out in two of four plastic silos anchored in the lake. The silos each enclosed a water column of 154 m^3 lake water with a surface area of 30 m^2. They were both treated with fertilizers, one with the proposed concentration exclusive of iron and the other with iron included. The experiments revealed slowly increasing chemical reactions in the iron-treated silo, forming colloids resulting in a 75% decrease in transparency

after a week (Olson, personal communication). In the other silo no such effects were observed within the first week. A strong growth increase in the phytoplankton was recorded in both silos, after a short period of inhibition. About nine weeks after application the maximum rate of gross production was recorded in the iron-treated silo with a value in surface waters of 180 times the original gross production (Olson, personal communication). Some doubt existed as to what degree the responses in the silos could be indicative of the lake itself due to the prehistory of the silo waters since the implantation of the silo in 1964 (Olsen 1965). Also, since no information concerning optimum fertilizer concentrations could be obtained from the pilot experiment, a bioassay analyzing effects of different quantities of fertilizers and specifying the importance of iron upon the rate of gross production in lake water was scheduled.

Different approaches have been used in measuring limiting nutrient factors in natural phytoplankton populations since Ryther and Guillard (1959) and Goldman (1960) applied the C-14 technique on similar problems for seawater and lakes, respectively. A review of this literature is given by Wetzel (1965) and Goldman (1965). The present investigation is in principle similar to the bioassays of limiting factors made by Ryther and Guillard (1959), since the analyzes are made on water enriched with different degrees of the whole spectrum of fertilizers and deals with the effect of removing one of the trace elements. It deviates, however, in that respect that a large volume of water was applied and that the analyzes of effects were carried out until a maximum level in the rate of primary production seemed to be reached.

MATERIALS AND METHODS

The bioassay was carried out in Fern Lake during the period 9 August–1 September 1966 in a series of fourteen 5-gallon glass bottles. Previous to the experiment the bottles were washed and rinsed in hot 2% Na_2CO_3 solution followed by hot 1% HCl solution and finally rinsed several times in lake water. Fifteen litres of lake water, collected 10 cm below surface from a raft anchored in the lake was filled into the bottles, and fertilizers added as follows:

Container No.	1 and 5	.....	No	fertilizers	added
	2 and 9	.....	¼ (c-Fe)	»	»
	3 and 10	.....	½ (c-Fe)	»	»
	4 and 11	.....	1 (c-Fe)	»	»
	6 and 12	.....	¼ c	»	»
	7 and 13	.....	½ c	»	»
	8 and 14	.....	1 c	»	»

where c refers to the composition and concentrations given in Table I, c-Fe to the same concentrations omitting iron.

The fertilizers were made from p.a. grade chemicals in five separate solutions in order to avoid precipitations:

Sol. 1	Sol. 2	Sol. 3	Sol. 4	Sol. 5
$MgSO_4$	$Ca(NO_3)_2$	H_3BO_3	$NH_4H_2PO_4$	$FeSO_4$
K_2SO_4	$CaCl_3$	$MnCl_2$	$NaHCO_3$	
$ZnSO_4$		$CoCl_2$		
		H_3MoO_4		
		KI		

The containers were plugged with rubber stoppers perforated with 1 cm glass tubing (30 cm long) with a bent plastic tube at the upper end. This system allowed free gas exchange and acted, at the same time, to guard the cultures from accidental contamination. Arranged in numbered sequence, the containers were left floating in the lake attached to a line anchored between the raft and the western shore (Fig. 2).

At intervals as given in Table II, parallel samples were collected from the containers into 125 ml Pyrex glass bottles for productivity measurements. Sampling was made with a squeeze-ball pump, after a thorough mixing of the content was secured by squeezing air into the bottom of the containers. The samples were placed in an incubator, injected with 2,5 microcuries C-14 as $NaHCO_3$, and incubated under artificial light for four hours (Steemann-Nilsen 1952). Similarly, bottles wrapped in aluminium foil were used to evaluate C-14 dark fixation during the same time. The temperature in the incubator was controlled to that of the lake. After four hours, the samples were filtered on Millipore filters (HA), preserved and removed of inorganic $^{14}CO_3^{--}$ by afterfiltering of 10 ml 10% formalin. Following drying in a desiccator, β counting

Fig. 2. Fern Lake bioassay. Experimental set-up.

of the MP filters was made on a Nuclear Chicago low-level β counter. The efficiency of the system was 6%.

Total alkalinity was determined from titrations with 0.02 N HCl in 200 ml samples, and the total available CO_2 was calculated as mgC/l using the conversion tables given by SAUNDERS, TRAMA and BACHMANN (1962). The rate of gross production under the standardized condition was calculated from the net count of the light and dark bottles as follows:

$$P = \frac{(cpm_L - cpm_D) \cdot 1.1 \cdot \text{total } CO_2}{R}$$

where cpm_L and cpm_D = counts per min. net from light- and dark-exposed samples,
R = dpm C-14 added times counter efficiency times correction for MP filter absorption (SAUNDERS *et al.*, 1962),
1.1 = correction for isotope discrimination and respiration.

Estimates of *in situ* rates of gross production were made according to BERGE (1958).

RESULTS AND DISCUSSION

The net cpm from the duplicate C-14 light incubator measurements are listed in Table II. Dark bottles were run only for one of the controls and for containers 13 and 14 (half- and full-fertilized lake water). These results are listed in Table III as net count per minute.

The data demonstrate generally good agreement between the duplicate C-14 measurements. On the 96% confidence level the average of the C-14 measurements are accurate to 14.8% on the whole, and for the first four days better than 7.7%. Within these errors of measurement, the results from the parallel series of experiments mostly agree very well. An exception demonstrate the duplicates with $\frac{1}{2}$ (c-Fe) fertilizer by the end of the experiment where the deviation from their mean is greater than 60%. The container with the higher of the values had, by the tenth day of observation, lost the stopper and glass tube protection. During the application of fertilizers to the lake initiated that day, contamination of this container likely has happened. In the following evaluations, this value has therefore been omitted.

No serious bacterial activity occurred in the samples, the dark fixation of C-14 being rather constant throughout the experiment (Table II), and constituting a decreasing significance in the C-14 measurements. It appears that day to day variations in the rate of photosyntesis occurred and had the same trend in the controls and in the other containers. Such variations were expected as effects of day to day changes in environmental

conditions. Since the effects presumably act proportionally on the activities in the cultures, they are eliminated in analyzing changes in the rate of gross production for each of the containers relative to those of the controls at the same time. Such data have been calculated as percentages of the average from the two controls and are listed in Table 1.

Table 1. C-14 fixation in the fertilized containers as percentages of that in non-fertilized lake water. Values are averages of duplicate measurements in four-hour light box incubations.
c = full proposed concentration of fertilizer in lake water.
c-Fe = full proposed concentration of fertilizer less iron in lake water.

	Time after fertilization						
	4 hrs	24 hrs	2 days	4 days	7 days	11 days	17 days
$\frac{1}{4}$.(c-Fe)	80	98	123	236	673	1223	1533
$\frac{1}{4}$.(c-Fe)	85	111	147	200	455	1400	1356
$\frac{1}{4}$.c	84	119	164	242	392	1688	2101
$\frac{1}{4}$.c	79	109	152	226	748	1647	2072
$\frac{1}{2}$.(c-Fe)	75	87	99	188	607	1804	10019
$\frac{1}{2}$.(c-Fe)	75	86	117	187	413	3231	2484
$\frac{1}{2}$.c	76	103	143	268	617	4131	5841
$\frac{1}{2}$.c	65	81	105	244	397	3038	3335
1.(c-Fe)	56	63	83	208	490	2817	7445
1.(c-Fe)	56	61	73	205	493	2505	8061
1.c	61	84	112	211	414	1227	20732
1.c	57	70	87	291	423	2583	15317

It is evident that no increase in the C-14 fixations was obtained in the fertilized containers before closely one day after application and in some instances, not before the second and third day after application (Fig. 3). On the contrary, inhibitions in the rate of C-14 fixations after four hours were evident in all the fertilized containers. The inhibitions, demonstrated by the maximum depressions in the curves are highly significant as confirmed by a t-test, and are increasing with increasing amounts of fertilizer applied. However, they are not significantly different for the series with and without iron as demonstrated by Table 2 and the diagram in Fig. 4 (left).

The intervals before the cultures have recovered increased with the amount of fertilizers used, but they were also significantly different for the series with and without iron: consistently, the iron-treated containers showed more rapid recovery (Fig. 4, right).

The inhibition was probably due both to sudden changes in the osmotic pressure of the water and to toxic effects from one or more of the elements introduced (Goldman 1965) and (Wetzel 1965). The difference

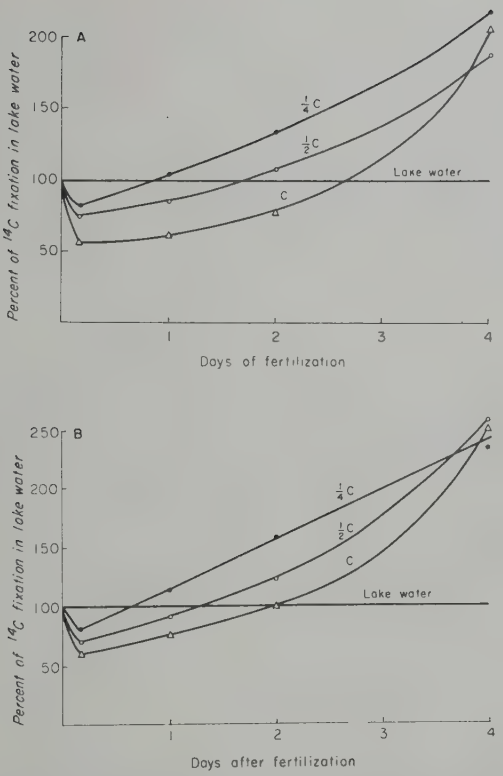


Fig. 3. Effects of fertilizers upon the rate of gross production during the first four days of the experiment. (A) without iron, (B) with iron, c = proposed concentration of fertilizers.

Table 2. Inhibition in C-14 fixation four hours after fertilization (%) and the time until recovery (hrs).

Concentration of fertilizer	Fertilizer inclusive of iron		Fertilizer exclusive of iron	
	% inhibition at 4 hrs.	Duration in hrs.	% inhibition at 4 hrs.	Duration in hrs.
$\frac{1}{4}$ c	17.6	20	18.5	16
$\frac{1}{2}$ c	25.1	40	29.4	31
c	43.9	64	41.0	46

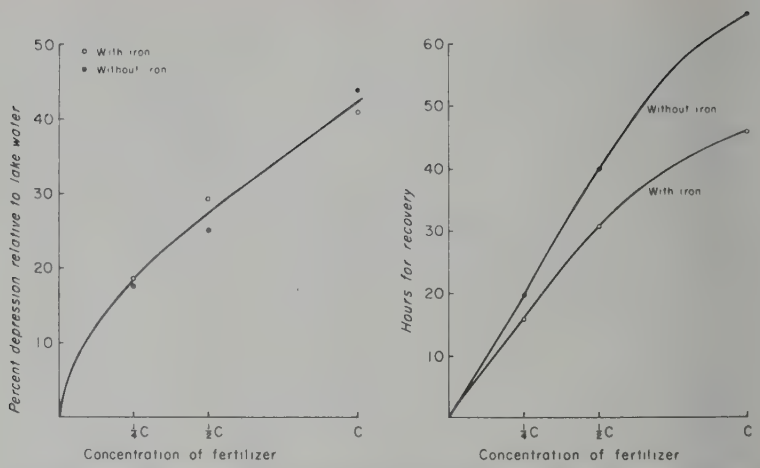


Fig. 4. Maximum inhibition of ^{14}C assimilation (left) and time before recovery (right) for different degrees of fertilization.
c = proposed concentration of fertilizers.

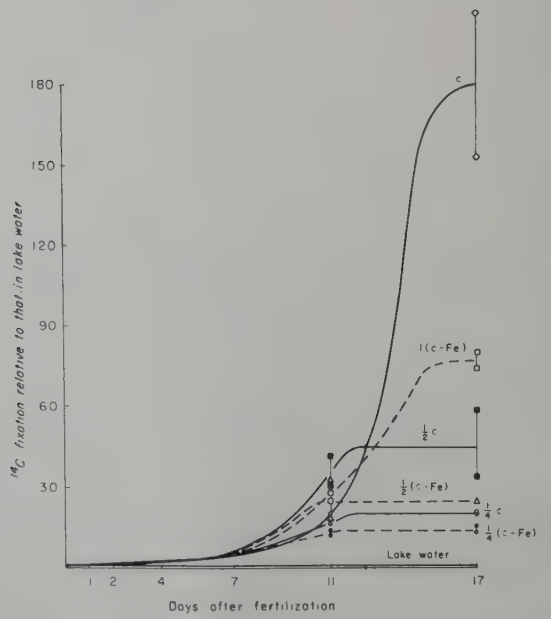


Fig. 5. Effects of fertilizers upon the rate of gross production.
c = proposed concentration of fertilizers, c-Fe = proposed concentration of fertilizers less iron.

in times when the inhibitions were effective in containers with and without iron, can be explained by the chemical reactions iron created in lake water, slowly forming colloidal materials less available to the plankton and with reduced effect on the osmotic pressure.

The data from Table 1 have been plotted in the diagram of Fig. 5 and growth curves are matched to the average of each of the duplicate series. It is evident that very high increases occurred in the rate of production in all the fertilized containers following a rather long lag phase. The final effects increased with increasing amounts and were higher in the series with iron than without. By the end of the experiment the production in the containers had apparently reached a steady state. For $\frac{1}{4}$ (c-Fe), $\frac{1}{2}$ (c-Fe) and c-Fe these levels seem to be limited by iron deficiency, since the corresponding series with iron all reached considerably higher values (Fig. 6). The highest effect was demonstrated in the container with full proposed fertilizers, where the rate of gross production had reached levels 180 times higher than in the non-treated lake water. Similarly, the rate of production in the fully fertilized containers without iron was 75 times that of lake water. The trend in the curves (Fig. 6) further indicates that stronger fertilizations than made both with and without iron would still increase the rate of production. The necessary quantities to reach maximum effects are not predictable from this experiment.

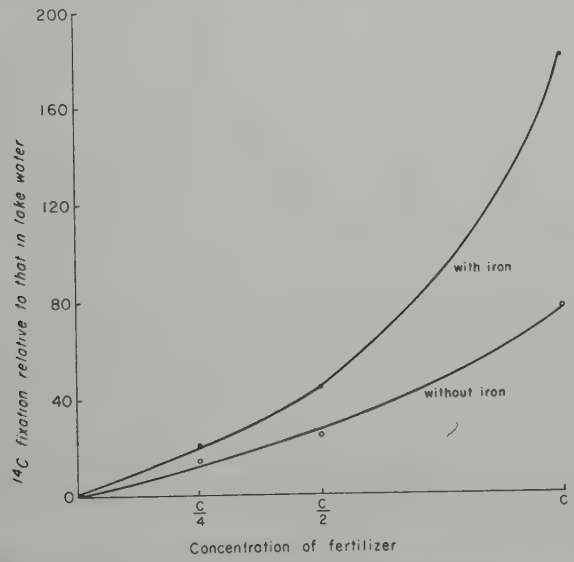


Fig. 6. Relations between rates of gross production in fertilized lake water with and without iron, seventeen days after treatment.

Using the average cpm for the duplicate experiments and 2.3 mg C/l as a representative average value for the total available CO_2 (Table IV), the ultimate rates of production reached in the differently treated containers have been calculated and are shown in Table 3.

Table 3. Rates of gross production in the fertilized and non-fertilized containers at the end of experiment. Values are average of the series.

	Av. cpm at 17 days	P mg C/m³ day	Rel. to lake water
Lake water	689	24.8	1.0
Lake water ¼ (c-Fe)	9,952	358	14
Lake water ½ (c-Fe)	17,113	924	25
Lake water 1 (c-Fe)	53,419	1923	78
Lake water ¼ c	14,376	518	21
Lake water ½ c	31,608	974	40
Lake water 1 c	124,190	4470	180

Although iron, where not applied, evidently became the limiting factor at the increased rates of productivity, it is interesting to note that increased applications of fertilizers without iron still caused increased growth. These findings seem to indicate that the iron possibly was available as contaminant in the other fertilizers. The present materials do not allow analyzes in this regard, and several possibilities for its explanation exist. It might be suggested that some other element partly can replace iron in matebolic processes or that the increased fertilizer concentraction changes the redox potential enough to alter the availability of naturally existing iron. Also, selection of different communities of organisms having different iron response rates might likely have occurred.

Care should be used in interpreting results from the experiments to the situation in the lake. The enclosure of small volumes of lake water in containers creates a serious change in the plankton ecology. Significant is the increased ratio of surface to volume of water; also the effects from changes in light intensity, wind mixing, and air temperature are seriously altered, and together these factors could influence both the composition and the activities of the primary producers. It is also obvious that the 15 litre samples do not represent a complete miniature of the ecosystem of the lake, and the intereffect by organisms in the containers is more or less artificial. However, using the results obtained relative to those from non-treated containers, the mentioned effects are minimized or, in some cases, even eliminated. It is thus felt that the general conclusions drawn

should be valid also to the lake itself under steady state conditions. It is interesting to note that the effect of full proposed fertilization with iron included was identical to the maximum effects recorded in the pilot experiment with the plastic silo. However, with respect to maximum effects, these should be considerably lower in the lake under natural conditions where dispersion and dilution would reduce the amount of fertilizers available to the primary producers.

The total rate of gross production of the lake is the sum of all the rates per unit volume at any place and depth, $P_{a,z}$. The latter is again related to the rate of gross production measured under standardized conditions (P_i) in the incubator the following way

$$P_{a,z} = P_i \cdot \frac{I_{a,z}}{I_i}$$

where $I_{a,z}$ = effective light at a,z and I_i = effective light in the incubator. The relation is valid as long as light intensities are below saturation for the producing population. For the major part of the lake's annual gross production, the relation is assumed to be valid. Forming the relation between the rates of production in fertilized water ($P'_{z,a}$) and in non-fertilized water ($P_{a,z}$), we have

$$\frac{P'_{a,z}}{P_{a,z}} = \frac{P'_i}{P_i} \cdot \frac{I'_{a,z}}{I_{a,z}} = \frac{P'_i}{P_i} \cdot \frac{T'}{T}$$

where T and T′ are the light transmissions of the water before and after fertilization. The total effect of the fertilization on the *in situ* rates of production at any place and depth of the lake is thus equal to the relative change in the rate of production at standardized conditions of the same sample times the relative change in light transmission of the water.

CONCLUSION

From the results presented, the following conclusions can be drawn.

Application to Fern Lake water of the proposed concentration of fertilizers, with and without iron, acts as a preliminary inhibitor upon the photosynthetic activity of the phytoplankton. For each of the two compositions of fertilizers used, the extent and duration of the inhibitions are nearly proportional to the amount of fertilizers introduced; addition of iron sulfate reduced the duration of the inhibition.

Following preliminary inhibition, a strong increase in the rate of production per unit volume and light occurs, increasing with increasing amounts of fertilizers. The trend of the results points out that the optimum effects will be reached with higher applications than proposed.

At the raised levels of photosynthetic activity, iron became a limiting factor if not applied. Application of iron raised the effect of fertilizers on the ultimate rate of gross production in the containers with an average factor of about 2. However, chemical reactions occurred in the water, forming colloidal materials which decreased the light transmission. The pilot experiments with Fern Lake water showed a 75% reduction in light transmission, a situation that seemed to persist over several months. Even with a twofold gain in the rate of gross production under standardized conditions relative to that of the iron-free parallels, the counteracting effect of the reduced transparency of the lake would cause a probable loss in the total gross production of the lake, as long as the colloidal materials persisted.

Since technical grade chemicals were planned to be used in the fertilization of the lake, it was anticipated that iron might be present as a contaminant, sufficiently not to become limiting.

The following advices for a successful improvement of the primary productivity can be given:

1. Fertilizers should be added to the lake in the full proposed concentration, exclusive of iron. By extrapolating the results, it seems evident that higher effects can be reached with higher applications.

2. Application of 100 ppb of iron (Fe^{2+}) increases the effect of fertilizers upon the rates of gross production under standardized light conditions. However, due to the effect of this amount upon transparency, it will reduce the integrated rate of gross production of the lake, and should, therefore, not be included.

3. After completed fertilization as above, bioassays with lake water should be repeated to investigate whether iron had become the limiting factor on the rate of production, and from similar experiments, possibly indicate quantities of eventual later additions.

4. The applications of fertilizers should be made sequentially, using one quart or less at a time, in order to minimize inhibition of the primary producers. For the same reason, rapid and thorough mixing with the whole water column seems important. The time intervals between applications should be three days or more to ensure rehabilitation in the plankton productivity between applications.

SUMMARY

1. With the object of predicting effects of different amounts of fertilizers, upon the rate of primary production in Fern Lake, a bioassay was carried out in a series of 14 twenty liters glass carboys.
2. The experiment revealed that the rate of gross production increased nearly proportionally with the amounts of fertilizers added and a maximum increase of 180 times the orginal rate of gross production was obtained.
3. When iron was included with the fertilizers colloidal substances were formed acting upon the transparency of the water. When it was excluded it became limiting on the rates of primary production.
4. It is demonstrated that due to reduced transparency the inclusion of 100 ppm iron would not increase the total primary rate of production of the lake any further.
5. Suggestions for the fertilization of Fern Lake are given.

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APPENDIX

Table I. Fern Lake water analysis together with the proposed addition of fertilizers. (Data from Olsen *et al.* (1967) and Olsen (1965).

Macro-elements mg/l	Lake Surface	Water Bottom	Proposed added (c)	Fertilizers Sources and Amounts
Ca	1.4	1.6	2.5	$Ca(NO_3)_2$ 5.12 mg/l
NO_3			3.8	
NH_4			0.1	$CaCl_2$ 3.46 »
Cl	2.8	3.1	2.2	
Mg	0.3	0.2	0.5	$MgSO_4 \cdot 7H_2$ 05.0 »
SO_4			2.6	
K	0.2	0.1	0.5	K_2SO_4 1.42 »
Na	1.5	0.5	1.0	$NaHCO_3$ 3.66 »
HCO_3			2.7	
PO_4-P	0.004	0.009	0.2	$NH_4H_2PO_4$ 0.74 »
Micro-elements μg/l				
B			10	H_3BO_3 57.1 μg/l
Co	6.4	11	10	$CoCl_2$ 22.0 »
I			50	KICl 65.4 »
Mn		24	50	$MnCl_2$ 179.8 »
Mo	0.2	0.2	10	$H_2MoO_4 \cdot H_2O$ 18.8 »
Zn	18.6	30.5	15	$ZnSO_4 \cdot 7H_2O$ 65.9 »
Cu	7.0	15	0	
Nl	5.4	2.5	0	
Fe	110	134	100	$FeSO_4.7H_2O$ 500 »

Table II. C-14 fixation in plankton from containers with untreated and with fertilized Fern Lake water.
Values in net CPM of C-14 assimilated from $2\frac{1}{2}$ μCi $^{14}CO_2$ per 125 ml of sample. Parallel runs in four hours light-box incubations.
c = full proposed concentration of fertilizer in lake water. c-Fe = full proposed concentration of fertilizer less iron in lake water.

Container # and contents	Time after fertilization: 9/VIII-4 hrs. CPM	10/VIII-1 day CPM	11/VIII-2 days CPM	13/VIII-4 days CPM	16/VIII-7 days CPM	20/VIII-11 days CPM	26/VIII-17 days CPM
No. 1: Lake Water	968	1379	1119	760	987	992	683
		1275		761	1077	937	664
5: Lake Water	1079	1143	1140	529	807	2062 (b)	714
	1151	1312	1304	542	906		694
2: $\frac{1}{4}$ (c-Fe)	858	1273	1491	1528	6927	12804	12031
	806	1223	1397		6007	11611	8992
9: $\frac{1}{4}$ (c-Fe)	853	1423	1716	1297	4678	14269	8992
	927	1419	1725	1297	4064	13682	9692
3: $\frac{1}{2}$ (c-Fe)	798	1124	1109		5831	17840	66650
	760	1094	1205	1221	5831	18165	71411
10: $\frac{1}{2}$ (c-Fe)	784	1106	1426	1276	4256	32241	18851
	688	1090	1323	1142	3673	32241	16376
4: 1 (c-Fe)	603	807	988	1580	4933	31233	52615
	588	808	941	1115	4487	24983	49963
11: 1 (c-Fe)	574	761	808	1352	4791	24376	55539
	591	798	888	1287	4678	25624	55539
6: $\frac{1}{4}$·c	897	1500	1943	1432	3593	15778	14476
	856	1545	1895	1704	3935	15856	14476
12: $\frac{1}{4}$·c	840	1349	1772	1424	9157	37020 (a)	13872
	813	1423	1788	1510	5218	31233 (a)	14689
7: $\frac{1}{2}$ ·c	762	1270	1646	1655	5033	45437	37020
	832	1351	1692	1818	6832	37020	43461
13: $\frac{1}{2}$·c	669	1016	1216	1588	3361	29395	23239
	687	1039	1241	1570	4312	31233	22710
8: 1·c	570	1091	1381	1397	4202	13141	142840
	698	1064	1342	1331	3756	11347	142840
14: 1·c	573	1349	1024	4098 (a)	4064	27761	111094

Table III. ^{14}C fixation in dark bottles during four hours incubator experiments. Values are net cpm of ^{14}C fixed from $2\frac{1}{2}$ μCi $^{14}CO_2$ per 125 ml sample. c = full proposed concentration of fertilizers.

	Time after start of experiment			
	2 days	4 days	11 days	17 days
Lake Water	94	90	110	103
$\frac{1}{2}$·c+ Lake Water	104	107	200	300
1·c+ Lake Water	113	93	219	269

Table IV. Physical-chemical properties in the experimental containers.

	Total Alk.	t°C	pH	CO_2mg C/l
Lake water, before exp.	8.20	22.5	7.2	2.26
Lake water, at end of exp.	7.92	23	6.65	2.87
Lake water with $\frac{1}{4}$ c fert. at and of exp.	9.08	23	9.30	2.00
Lake water with $\frac{1}{2}$ c fert. at and of exp.	9.60	23	9.80	2.11
Lake water with 1 c fert. at end of exp.	10.20	23	9.70	2.24
Average total CO_2 as mg C/l =				2.30

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COMPARISON OF PACIFIC SARDINE AND ATLANTIC MENHADEN FISHERIES

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INTRODUCTION

The rise and fall of the North American Pacific coast sardine fishery is well known. Once the most important fishery in the western hemisphere in weight of fish landed, it now produces virtually nothing. The meal and oil industry based on the Pacific sardine (*Sardinops caerulea*) resource no longer exists. The sardine fishery (Fig. 1A) began in 1915, rose fairly steadily to its peak in 1936 (with a dip during the depression), maintained an average annual catch of more than 500 000 tons until 1944, then fell off sharply. Annual production has not exceeded 100 000 tons since 1951, and commercial sardine fishing now is prohibited in California waters. A much smaller fishery for the southern sub-population developed off Baja California in 1951.

The decline of the west coast sardine fishery gave impetus to the much older menhaden (*Brevoortia tyrannus*) fishery (Fig. 1B) along the Atlantic coast of the United States. Fishing for Atlantic menhaden began early in the nineteenth century. From the 1880's until the middle 1930's the annual catch varied around about 200 000 tons. In the late 1930's annual landings began to increase and from 1953 to 1962 inclusive remained above 500 000 tons. The peak year was 1956, with a catch of nearly 800 000 tons. After 1962 the catch began to fall off sharply, reaching a low of less than 250 000 tons in 1967.

The remarkable similarity in history of landings of the two species is illustrated in Fig. 1. If the sardine curve is shifted in time about twenty years the coincidence is startling (Fig. 1C). The following questions arise:

1. Is the Atlantic menhaden fishery doomed to extinction?

Contribution given in honour of Gunnar Rollefsen at his 70th birthday.

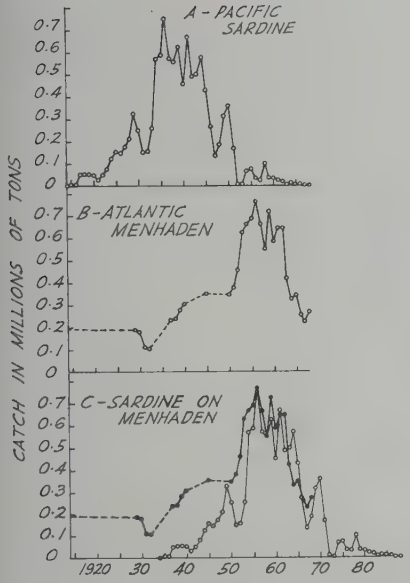

Fig. 1. Historical record of Pacific sardine landings (A), Atlantic menhaden landings (B), and sardine landings shifted twenty years and superimposed on menhaden landings (C). Data from Ahlstrom (1960), Henry (1968), and Statistical Digests of the Bureau of Commercial Fisheries.

2. Is there anything in the history of the Pacific sardine fishery or in knowledge of the biology of the species that would lead to inferences about the future of the menhaden resource and its fishery?

3. Does the history of the sardine fishery offer any lessons that might help the menhaden industry or other fishing industries anywhere in the world to avoid the fate of the sardine industry?

In this paper these questions are examined only briefly.

COMPARISON OF LIFE HISTORIES

Both species have relatively wide ranges of distribution along coasts that trend generally north and south (Fig. 2). The Pacific sardine once ranged from south-eastern Alaska to the Gulf of California (55° to 23° N. Lat.). The Atlantic menhaden has been taken from Nova Scotia to southern Florida (46° to 23° N. Lat.). It does not pass around the southern tip of Florida into the Gulf of Mexico, but another species, *Brevoortia patronus*, supports the important menhaden fishery in the Gulf.

Within these geographic ranges, samples of the commercial catch of Pacific sardine and Atlantic menhaden usually contain larger and older fish with increasing latitude. Not only do the older fish go farther north, but also apparently the larger fish of each age, for the apparent growth

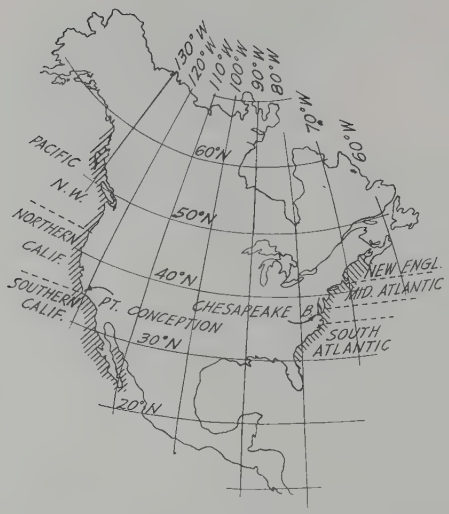

Fig. 2. Geographic distributions of Pacific sardine and Atlantic menhaden along North American coasts.

rate increases from south to north (Fig. 3). Both species are found in northern oceanic waters usually only in summer. Usually, adults are found farther north than young, and young farther north than the pelagic eggs. Adult Pacific sardines and juvenile Atlantic menhaden sometimes spend the winter in northern inlets or tributaries. From these observations it has been inferred that most spawning occurs towards the southern part of the range of each species and that most of the mature fish make an annual northward migration in spring and summer, returning south in late fall and winter, and moving farther northward with increasing size and age. These inferences have been confirmed by tagging. In

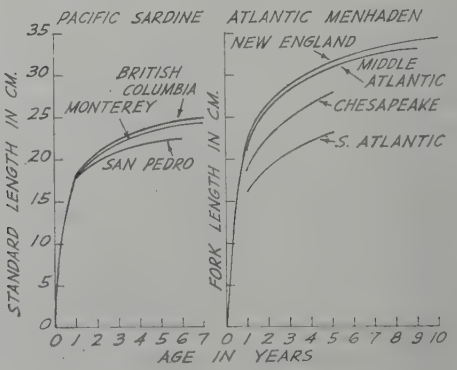

Fig. 3. Apparent growth rates of Pacific sardines and Atlantic menhaden from commercial catches at different latitudes.

common with many clupeioid fishes there is also a tendency for older and larger fish to be farther offshore. Both species are divided into subpopulations, which do not intermingle completely, although their geographic ranges overlap considerably.

Plankton studies have confirmed the inferences about major spawning areas, but Pacific sardine spawning progresses in a wave from south to north, winter to summer, whereas Atlantic menhaden spawning apparently progresses from north to south, summer to winter. The location and intensity of spawning of both species may vary widely from year to year, and survival to the stage of recruitment into the commercial fishery varies widely.

Scientific studies of the Pacific sardine and its fishery have been under way since the early days of the fishery, and the biology and ecology of the species and the response of the stocks to fishing are reasonably well understood. Substantial continuing studies of the Atlantic menhaden and its fishery began little more than a decade ago, and scientific investigations are still not adequate to obtain all the information necessary to understand the population dynamics and ecology of the species and to stabilize the economics of the fishery. For both species funding of scientific investigations was difficult to obtain until substantial declines in the resource and the catch created responsive political climates.

COMPARISON OF THE FISHERIES

Although the Pacific sardine fishery began off California, toward the southern part of the geographic range, and the Atlantic menhaden fishery began to the northward, off New England, the reaction of the two resources to fishing has been similar. As could have been predicted from knowledge of the biology of the species and of the known effects of a developing fishery on fish stocks, fishing reduced the life expectancy. Thus the northern fisheries were affected first (Fig. 4). The peak of the sardine fishery in the Pacific North-west covered the period from 1929 to 1943, and the fishery collapsed before 1950. In northern California the peak was from 1934 to 1944 and the collapse in the early 1950's. In southern California landings were substantial from 1934 to 1950, with a peak in 1950, and fishing continued at a lower level of catch into the early 1960's, after the industry in the north had suspended operations.

The history of menhaden landings has been similar (Fig. 4). In New England the catch reached a peak in 1899, then fell off virtually to nothing in the 1930's and 1940's. There was a resurgence in the 1950's, which lasted until about 1960. The peak of the fishery in the middle Atlantic region covered the period 1953 to 1963, and by 1965 that segment

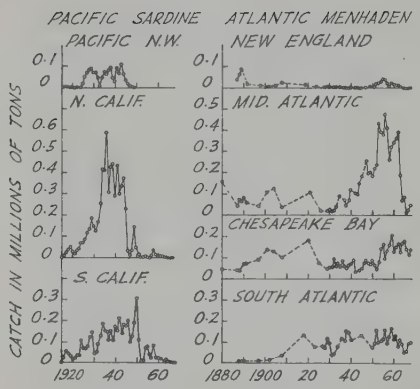

Fig. 4. Historical catch records of Pacific sardine and Atlantic menhaden at different latitudes.

of the industry was virtually dormant. In Chesapeake Bay a high level of catch has been maintained since 1954, with some decline in the last two years. The catch in the Chesapeake has been maintained only at the expense of a substantial increase in fishing effort. In the area south of Chesapeake Bay the catch has fluctuated about the same level since 1936.

The decline and collapse of both fisheries from north to south is demonstrated better by considering the trends in percentage of the total catches taken in the northern parts of the species range. For the Pacific sardine the northern area includes waters north of Point Conception, for the Atlantic menhaden it is the area north of Chesapeake Bay. From the peak of the fishery in the decade beginning about 1934 the percentage of the sardine catch taken to the north fell from about 80 per cent in the late 1930's to zero in the late 1960's (Fig. 5). From the peak of the Atlantic menhaden fishery in the middle 1950's the percentage of the total catch taken north of the Chesapeake fell from over 70 per cent in 1953 to less than 20 per cent after 1965 (Fig. 5). For both fisheries, once the peak was reached the percentage of the catch taken in northern waters was a direct

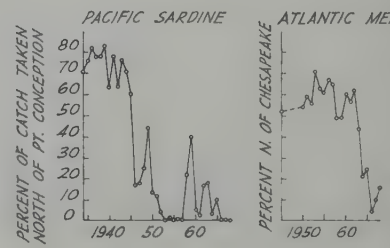

Fig. 5. Trends in percentage of the total catches of Pacific sardine and Atlantic menhaden taken in northern waters as each fishery declined from its peak.

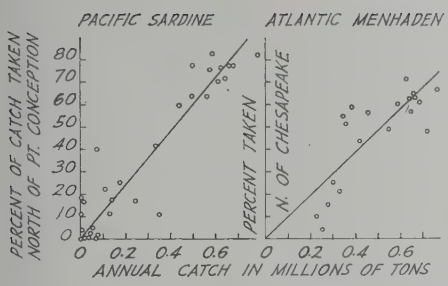

Fig. 6. Relation between total annual catches of Pacific sardine and Atlantic menhaden and percentage of the catch taken in northern waters.

function of abundance as reflected in the total catch (Fig. 6). Such declines do not necessarily connote overfishing, but they do throw the bulk of fishing effort on the younger fish to the south, and increase the risk of overfishing.

ROLES OF OTHER FACTORS DETERMINING ABUNDANCE

The evidence is strong that there has been no reduction in total biomass of pelagic fishes in the California Current System. The drop in sardine abundance has been offset by increases in other species, especially anchovy. McHugh and Ahlstrom (1951) suggested that fuller utilization of species such as anchovy, saury (*Cololabis saira*), and jack mackerel (*Trachurus symmetricus*) should be encouraged. The possibility exists that similar compensatory changes may be taking place in the environment of the Atlantic menhaden but the research program has not been broad enough to determine if this is so. Several species could be involved in such ecological adjustments, including sea herring (*Clupea harengus*), thread herring (*Opisthonema oglinum*), and jacks (*Caranx crysos*, *Trachurops crumenophthalma*), to name just a few. The catch of sea herring has increased steadily in the last few years, and the fishery (mostly by nations other than the United States) now extends south to Cape Hatteras (about 35° N. Lat.). Whether this southern herring fishery has been made possible by an increase in abundance favored by the menhaden decline is not known. The relationship between menhaden abundance and biomass of other species such as thread herring also is not known. It is important that such ecological interactions be understood.

LESSONS TO BE LEARNED FROM THE SARDINE FISHERY

Many people have contributed to scientific knowledge of the Pacific sardine resource and the effect of fishing on it. Particularly useful references are the work of Ahlstrom (1960, 1966), Clark and Marr (1955),

Marr (1960, 1963), Murphy (1966) and Radovich (1962). Scientific studies have shown beyond reasonable doubt that the sardine stocks were reduced by a combination of intense fishing and poor spawning success, and that the Pacific northern anchovy (*Engraulis mordax*) invaded the environmental niche vacated by the sardine. It has been estimated that the sardine resource has dropped to 5 per cent or less of its former biomass, and that the standing crop of anchovy has increased at least twenty-fold over the same period.

A fishery based on a single species, highly variable in abundance, is not likely to be a stable fishery. If there is a profitable market for the product, capital investment in boats, fishing gear, and processing plants will grow. The exigencies of natural fluctuations in abundance, and the stimulating effect on survival to recruitment caused by reduction of the total stock, make it highly probable that as the fishery develops towards maturity, two or more strong year classes will follow each other in a relatively short span of time. Encouraged by this unusually high productivity the industry will continue to enlarge its capacity to catch and process the fish. Inevitably the time will come when biological productivity of the species drops from environmental causes. Since in a fully developed fishery the standing stock usually is about half the size of the unexploited population, other species may be given a competitive advantage which may inhibit production of strong year classes in the species being fished. Moreover, the time lag of a year or two in building vessels and plants usually may provide maximum catching and processing capability when the resource is already declining. In the absence of effective fishery regulation disaster is probably almost inevitable. Even with an effective regulatory mechanism, backed by adequate scientific knowledge, management is far from easy. There is no single optimum sustainable yield in a widely fluctuating resource. Only in certain salmon fisheries has a widely flexible scale of annual catch quotas been applied successfully.

When the sardine fishery was at its peak, there was no interest in alternative resources. Each species has different habits and reactions to fishing gear, and the industry had no time to waste in learning how to catch other species when sardines were present. As the resource declined many units in the fleet were preoccupied with searching for the absent schools of sardines, buoyed by the persistent optimism of fishmen that next year would be better. This optimism was strengthened by a brief resurgence of the resource in 1949 and 1950, and by a lesser increase in the middle and late 1950's. The concern of industry is illustrated by its action in imposing a voluntary tax on landings, the funds to be used in support of research. The industry was aware of the existence of a substantial anchovy resource, and in 1953 landed more than 40 000 tons.

But they were unable to develop a viable market for canned anchovies, and opposition to use of anchovies for oil and meal was already strong.

As the sardine stocks declined, the political climate for developing alternate resources for the fish meal and oil industry on the Pacific coast was becoming more difficult. The powerful sportfishermen's organizations in the State of California, convinced that disappearance of the sardine was reducing the availability of forage fishes, successfully sponsored restrictive legislation and regulations. This placed increasing restrictions on the commercial sardine fishery and also made it difficult to develop an anchovy fishery. Commercial fishing for sardines in California waters is now prohibited entirely. Attempts to develop a viable commercial anchovy fishery in the last few years led to a proposal by the scientists for an annual quota of 200 000 tons, with provision for carefully controlled scientific monitoring. This quota was selected because it was about the smallest catch that could be expected to produce a measurable effect on the resource, yet offer no threat of overfishing. A much lower quota of 75 000 tons finally was adopted, but this small quota has never been reached, partly because it has been divided into sub-quotas by areas, partly because the uncertainty of being permitted to continue a commercial anchovy fishery may have discouraged commercial fishermen from acquiring modern, efficient catching equipment, but probably mainly because such a small quota offers little promise of developing a profitable industry. If a fishery for anchovy and other suitable pelagic species had been allowed to develop while the sardine resource was still in good condition there might still be a prosperous fish meal and oil industry on the Pacific coast. It would be unfortunate for American fishermen if fishermen of other nations were to demonstrate successfully that these unutilized resources are abundant and can be taken economically in international waters.

As often happens in fishery investigations, scientific studies were not adequately supported until the sardine resource was already well on its way to obscurity. When the expanded investigations of the California Cooperative Oceanic Fisheries Investigations (CalCOFI) began in 1948 the catch was down to about 25 per cent of its former levels. CalCOFI has sponsored an impressive series of scientific studies, which have advanced fishery science considerably, but this knowledge came too late to be of much value to the sardine industry. The ecological implications of this valuable work should not be ignored in funding, investigating, and managing other fisheries.

PRESENT CONDITION AND FUTURE PROSPECTS FOR ATLANTIC MENHADEN

The literature on the menhaden fishery is by no means as extensive as that for the sardine. The principal references used were Henry (1968) and Reintjes (1969).

Although it has not been demonstrated conclusively that the menhaden resource has been overfished, the striking similarity in trend of landings should give cause for concern (Fig. 1). It should be noted especially that the sardine catch improved substantially for a period of two or three years following the poor catch of 1947. This caused most people in industry, and some scientists, to say that the sardine decline was temporary. Actually, no one knew at that time exactly what was happening. The catch fell almost to nothing in 1952 and 1953, and following two brief and much smaller upsurges in 1955 and 1958, the fishery soon collapsed. If the Atlantic menhaden fishery were to follow the same trend, the point of collapse could come as early as 1972, and certainly no later than the early 1980's (Fig. 1C). This cannot be regarded as a valid prediction, but the possibility should not be dismissed lightly.

The menhaden industry was encouraged in 1968 by an increase in the catch in the middle Atlantic and Chesapeake areas. The middle Atlantic catch was almost double the catch in 1967 and the Chesapeake catch increased by more than 20 per cent. There is some evidence that the 1966 year class was larger than any year class since 1963, and this could account for improved catches in 1968, but the 1966 and the 1963 year classes were much smaller than the dominant year class of 1958 and the other large year classes that supported the peak years of the fishery.

The Atlantic menhaden fishery has not declined to quite the low level that finally led to increased scientific attention to the sardine resource some twenty years ago. Indeed, it cannot be predicted with assurance that the Atlantic menhaden fishery will take the same course as the sardine fishery, although there is no scientific basis for optimism. To some it may appear that neither the industry nor fishery managers have drawn any lessons from the history of the sardine fishery. The industry remains optimistic that the situation will improve, and has hailed the improved catches of 1968 as evidence that the decline may have been temporary, especially in the area north of Chesapeake Bay. The three peaks in sardine catches after 1947 were also accompanied by increased catches north of Point Conception (Fig. 4) as would be expected from the migratory habits of the resource. Meanwhile, sport fishermen on the Atlantic coast are becoming increasingly concerned about the menhaden fishery, and pressures for restrictive legislation are increasing in each session of several State legislatures.

Murphy (1966) estimated that the maximum sustainable yield of Pacific sardines for the period ending in 1946 was about 470 000 tons a year. From 1937 to 1945 the sardine fishery took an average annual harvest of about 570 000 tons, or about 100 000 tons per year over the estimated surplus production. This intense fishery was removing about 79 per cent of the stock of sardines of commercial size each year. Considering the geographic range of the Atlantic menhaden resource as compared with the Pacific sardine, the similarity in life histories, and the remarkably similar patterns of landings during the peak years of the two fisheries, it would have been prudent to assume that the maximum sustainable yield of Atlantic menhaden would not exceed 470 000 tons annually. The average catch of menhaden from 1953 to 1962 inclusive was about 658 000 tons. Thus, if the assumption about maximum sustainable yield of menhaden is tenable, the stock was being overfished by about 40 per cent.

Concentration of the fishery for menhaden or sardine in the southern part of the species range has other disturbing biological and economic implications. This forces the fishery to take increasing proportions of younger fish, many of which have never spawned. A menhaden fishery conducted exclusively north of Chesapeake Bay would take larger and older fish, increasing the odds that substantial numbers would be able to spawn at least once before capture. Moreover, if menhaden are like other clupeid fishes, the average oil yield should be considerably greater in northern waters, but the yield of meal should not be substantially less. Thus, the economic return per unit weight of fish could be greater. It is unlikely that the industry in the south would be willing to restrict its operations in favor of operators in more northern waters, although this might prove to be the simplest way to manage the fishery. The question has not been examined carefully, but it would merit study.

The menhaden industry, with government assistance, has been giving attention to the need for alternate resources, not only along the Atlantic coast, but also in the Gulf of Mexico, where menhaden catches have been dropping since the early 1960's. Thus, some of the lessons have been heeded, but they may have been heeded too late and with too little sense of urgency by industry and scientists alike. For example, no scientific evidence is available to show whether other species in the same geographic areas are reacting in any way to the changed abundance of menhaden. Essentially, history may show that the menhaden industry today is at the critical stage reached by the sardine industry two decades ago. Here is an opportunity for government and industry to build on the experience of the sardine industry, before it is too late, in a joint effort to broaden the resource base of the Atlantic fish meal and oil industry and to take

advantage of the considerable advances in fishery science that have been made since the end of World War II.

It is not necessary to wait until indisputable scientific evidence is available before taking action to manage a fishery. History has shown that such caution usually leads to disaster. The history of the Pacific sardine fishery, and present knowledge of the ecology of the resource, suggest that the industry might have been prospering today if the knowledge necessary for appropriate action had been available, and such action had been taken. The menhaden industry has taken some tentative voluntary steps in this direction. It is to be hoped that industry will recognize the need to continue seeking a rational fishing policy.

SUMMARY

The Pacific sardine resource, which once supported an important American fishery, declined abruptly in the late 1940's and early 1950's, and the fishery is now defunct. Scientific research during the peak of the sardine fishery and subsequent to the decline has demonstrated fairly clearly that the cause was overfishing, fluctuations in abundance from natural causes, and invasion of the vacated niche by the Pacific northern anchovy. It has been concluded that it may not be possible to harvest a sustainable yield from a highly fluctuating resource like the Pacific sardine, for the reduced population will yield available energy to other ecologically similar species. Thus, the concept of a broad resource base made up of several species may be essential to the economic viability of most fishing industries. Perhaps the best documented example of the effect of selective fishing on the ecology of a large body of water is the history of the fishery resources of Lake Michigan (Smith 1968).

About twenty years later the Atlantic menhaden fishery went through a remarkably similar cycle. The northern fishery is virtually defunct, but the southern fishery is still in operation. The total annual catch now is a little more than one-third as large as the average catch from 1953 to 1962. Although it has not been demonstrated that the Atlantic menhaden resource is overfished, it might be prudent to borrow from the experience of the sardine industry and develop management plans accordingly. An important consideration would be to determine as soon as possible which species in the environment of the menhaden are utilizing the energy released by the decline of the resource. It is unlikely that fishery management in the ocean will ever be generally successful if action is postponed until absolute proof of overfishing is available.

ACKNOWLEDGMENTS

My interest in herring-like fishes and their variations in abundance was stimulated very early in my professional life by the work of Dr. Gunnar Rollefsen. I am honored to dedicate this paper to him.

It was not possible to make a thorough literature review in preparing this article. I believe I have consulted most of the major recent comprehensive papers on pertinent aspects of the two fisheries. If I have missed important papers or have not given appropriate emphasis to the recent literature it was not intentional. I apologize to authors whom I may unwittingly have slighted.

I am indebted to John C. Marr, Kenneth A. Henry, and Milner B. Schaefer for reviewing the manuscript.

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THE FLUCTUATION OF YEAR-CLASSES AND THE REGULATION OF FISHERIES

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INTRODUCTION

Fishermen contrast the considerable regularity in the positions of capture of fish with the variation in quantities caught at those positions from year to year. The regularity is that of the migratory circuit from spawning ground to feeding ground and back again (Harden Jones 1968); for example, spawning cod have been caught in the Vestfjord for centuries (Rollefsen 1956) and, since the thirties, fish of the same stock have been caught on the Svalbard Shelf west of Bear Island in early June. Similarly, the East Anglian herring have been caught in October and November off Lowestoft and Yarmouth for centuries as they migrated southward to spawn. But both stocks, cod and herring, vary from year to year due to differences in the recruiting year-classes. These differences can be grouped in three categories:

1. Annual changes due to density independent effects.
2. Density dependent changes following changes in stock.
3. Long term changes associated with changes in climate.

THE THREE CATEGORIES OF VARIANCE IN RECRUITMENT

Fig. 1 shows how the three categories of variation may be represented on a stock and recruitment curve. The curve of recruitment cuts the bisector at the point at which stock replaces itself in recruitment; in effect, it is the level of stock about which it stabilizes itself under natural conditions without fishing. Variance in recruitment about the stock and recruitment curve is represented on the ordinate (a) below the replace-

Contribution given in honour of Gunnar Rollefsen at his 70th birthday.

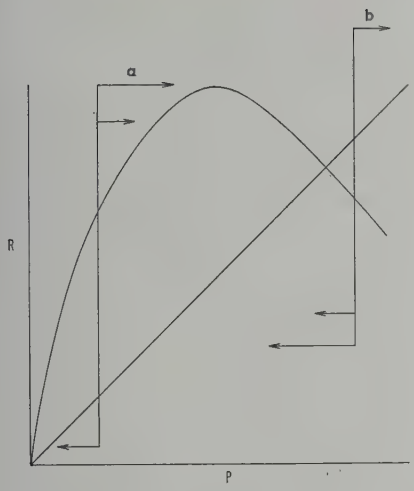

Fig. 1. The three sources of variance in recruitment shown on a stock and recruitment curve; see text for discussion.

ment point in stock and on the ordinate (b) above it in stock. Both represent the first category of fluctuation, variance in recruitment from year to year due to density independent causes. The second category is represented by the stock and recruitment curve itself; as stock increases, the recruitment per unit stock decreases and this is the effect of density dependence. The third category of variation occurs if recruitment falls below stock when stock is very low and then downward instability in stock is generated, which is represented in Fig. 1 by the variance of recruitment on the ordinate (a) falling below the bisector; an upward instability—at high stock—can be generated in an analogous way by the variance of recruitment on the ordinate (b) appearing above the bisector. If such instabilities occur randomly, subsequent recruitments must return the stock in the direction of stability. If, however, they occur in sequence, the stock collapses or expands, which are the conditions under which climatic change can affect the fluctuations.

PROCESSES DURING THE PERIOD OF LARVAL DRIFT

To survive, the larvae need food, not only when the yolk-sac is exhausted, but all through their lives during the period of larval drift. Although algae are often found in the guts of larvae at the first stages of active feeding, the baby fish subsist in the main on copepod nauplii (Lebour 1918a, b and 1919) and their analogues. In temperate seas, the production of nauplii is linked to the feeding of adult copepods in the early stages of the production cycle (Marshall and Orr 1952). So food

is available to fish larvae at a fairly early stage in the cycle and this accounts for the link shown below between the herring populations and the form of production cycle.

However, the production cycle is variable in timing, in amplitude and in spread (Colebrook 1965) and if fish in temperate seas spawn at relatively fixed seasons (Cushing 1969a) then the food available to the larvae must vary as the cycle varies. The variability of the production cycle tends to increase with depth of water as it depends much upon the vagaries of the depth of mixing, largely governed by wind strength and direction. This accounts for the greater variability in recruitment observed in stocks living over deep water in temperate seas. In the relation of spawning and the production cycle, time is critical to the survival of the larval fish, and the observed variance implies that the major processes determining recruitment may lie between spawning and nursery ground.

The separation of the three categories of variance in recruitment is perhaps a little artificial as all three may be but facets of a single set of processes. In temperate seas, the variance of recruitment to herring stocks tends to increase with depth (Cushing 1967) and it has been shown that the three groups of autumn-, winter- and spring spawning herring stocks are associated with three forms of production cycle in the north-east Atlantic (Cushing 1967). The increased variance in recruitment with depth can be associated with increased instability in the timing of the production cycle providing food for the larval fish. The two results lead to the conclusion that the processes determining the major proportion of larval mortality must lie between spawning ground and nursery ground because the production cycles on the nursery ground must differ from those in the open sea, if only because of differences in depth. The argument depends on the biology of the herring; it can be extended to other species when it is recalled that fish of many species spawn at about the same time. For example, in the Southern Bight of the North Sea, when herring spawn there so do cod, whiting, dabs, sandeels and plaice.

Of the three sources of loss to which the larvae are subject, predation, diffusion and advection, it is likely that predation is by far the most important. The loss rate of plaice larvae in the Southern Bight of the North Sea is 80 per cent per month as an apparent mortality (Harding, in preparation), which is considerably more than might be expected from the physical causes. It is assumed that a larva, which has moved out of the larval drift and fails to reach the usual nursery ground, is lost to the stock, i.e. it fails to return to the native spawning ground as an adult. The real question is how can predation in the larval drift effect the three categories of fluctuations which are illustrated in Fig. 1.

The fish larvae feed and as they feed they grow. As they grow they

swim more quickly and reduce the chance of predation. If they fail to feed adequately they swim more slowly and the chance of predation is increased. So with constant predation, variations in mortality rate can be generated merely by differences in the availability of food. Then, variations in stock change the food availability and so the mortality rate generated by the predators is also density dependent. The assumption of constant predation may appear to be unreal, especially if a particular predator is in view. The fish moves through three trophic levels as it grows and within any one level it is likely to be subject to a succession of predators, each larger than the last, but each less numerous. The differences between densities of each predator may tend to average out and then the low variability of recruitment as proportion of total mortality between egg and adult is not surprising. It is possible, in an evolutionary sense, that the fecundity of a fish stock is a function of the mortality generated by the network of predators along the larval drift and on the nursery ground.

VARIANCE OF RECRUITMENT ABOUT THE STOCK AND RECRUITMENT CURVE

Although it is unlikely that year-classes are completely determined during the period of larval drift, because by then only a small fraction of life to recruitment has elapsed, much of the variance of recruitment might be attributed to variance in food availability, itself due to variation in the timing of the production cycle. Many attempts have been made to correlate recruitment with environmental factors, but usually they have failed. An important exception is the correlation of catches of cod at Lofoten with the number of rings on pine trees in northern Norway for a long time period (Ottestad 1942). The reason for success is that a well-known result of climatic change was correlated with the catches. A particular cause was not specified, like the strength of a wind from a given direction over a very broad area, but a general result was indicated. The variation in the production cycle is governed by the rate of change of the algal reproductive rate, which in its turn is controlled by the rate of change of the ratio D_c/D_m, where D_c is the compensation depth and D_m is the depth of mixing (Cushing 1962). Very roughly, this ratio is affected by changes in sunlight and by changes in wind strength and direction. It follows that these climatic parameters need be sampled only on the track of the larval drift from spawning ground to nursery ground.

Correlations between recruitment and winds were often successful for a period of years, after which they failed catastrophically. Any examination of trends in wind strength and direction, at one position at the same

season for a long time period, shows that there are shifts in strength and direction of wind all the time (Dietrich 1954). Hence to take wind strength variations from a single direction is to ignore perhaps the most important source of variation. In temperate seas, the track of larval drift is usually not far from a coastline, where a small shift in direction can have considerable effects.

A considerable source of variation can lie in the stock and recruitment curve itself. That for the Arctic cod is dome-shaped as has been shown by Garrod (1966). At middle levels of stock, average recruitment is considerably higher than at low levels and at high levels. In contrast, the curve for the East Anglian herring is not far from a linear one, with only a slight dome before it passes through the replacement point. Differences in recruitment at different levels of stock are considerable. So if we need to know the true relationship between recruitment and environmental factors, recruitment should be measured as deviation from the stock and recruitment curve. If it is believed that such a curve should be fitted from the data on recruitment and data on stock only, then the argument is circular. The circle can be broken if it is assumed that there is a curve characteristic of any fish species and that differences, for example between that for the Arctic cod and that for the East Anglian herring, are real and not merely statistical fantasies.

AN INDEX OF DENSITY DEPENDENCE AND ITS CONSEQUENCES

Cushing (1969b) has examined the possible stock and recruitment curves for thirty-one stocks. No differences between constants were found using the Ricker equation (1954, 1958) or the Beverton and Holt (1957) equation. An index of density dependence, b, was calculated from the equation $R = KP^b$ (where R is recruitment, P is stock, and K is a constant), used at mid to high stock levels. It was found that $b \alpha \bar{f}^{1/3}$, where $\bar{f}$ is the average fecundity of the stock, over a range in b from $b = 0.8$ to $b = -1.95$. In effect, this means that there is a series of curves ranging from the near linear curve of the East Anglian herring to the pronounced dome of the Arctic cod, each of which is specified by the fecundity of the fish. Fecundity is a function of weight, and density dependent growth decreases with size in fish (Raitt 1939, Iles 1967, Southward 1967) and so it is effectively independent of the index, i.e. density dependence must be achieved in density dependent mortality. Thus, we return to the point that in an evolutionary sense, fecundity is a function of the network of predators along the track of the larval drift. Because there is a fixed

quantity of eggs available, fecundity may be regarded as a homeostatic mechanism which creates stability in a variable environment.

Larval density is a function of the density of spawning females and of fecundity. With fish like the herring which do not grow much during their mature lives, fecundity must play less part in determining larval density than the density of spawning females. With fish like the cod which grow a great deal as mature animals, fecundity may not stabilize the population: a stock at the replacement point which suffers a recruitment failure must suffer an increase in average weight and fecundity, which by itself must generate instability. At the same time, after a recruitment failure, the density of spawning females must decline which will generate greater recruitment per unit stock which is a stabilizing change. So it is likely that stock differences affect larval density merely through differences in the densities of spawning females. Then fecundity controls differences in the degree of density dependence between stocks as might be expected from its supposed homeostatic character of evolutionary origin.

A DIFFERENCE BETWEEN HERRING-LIKE FISHES AND COD-LIKE FISHES

On Fig. 1 variance in recruitment due to differences in stock density is expressed in the stock and recruitment curve itself. In larval density, differences in stock affect the availability of food, more being available to the larvae at low stock and less at high; and from the preceding argument such differences within a stock are generated by differences in the densities of the spawning females rather than fecundity. The question of how much of the variance of recruitment is due to density dependent causes and how much to density independent causes cannot readily be answered in general terms. However, D. J. Garrod has analysed the variances in the recruitment of spawners to the Arctic cod stock and has separated those due to environmental changes and those due to stock changes. Because the stock and recruitment curve for the Arctic cod is markedly dome-shaped, it is likely that for other fish stocks the ratio of density independent variance to density dependent variance may be greater. Indeed, it is possible that the ratio is correlated with the index of density dependence, or with fecundity. As further consequence, it might be concluded that the herring-like and salmon-like fishes were more vulnerable to environmental change than the cod-like fishes. Another way of saying the same thing is that the cod-like fishes have a greater capacity for stabilizing their populations than have the herring-like fishes. The stock of the Arctic cod has varied in quantity to some extent during the long centuries of its recorded existence (Rollefsen 1956). In contrast, the Norwegian herring

fishery, which is worked in a somewhat less adverse environment than the Arctic cod, has suffered a series of temporary extinctions over about the same historical period (Devold 1963).

The dramatic changes in pelagic fish stocks are exemplified well by the Norwegian herring periods which have been correlated with ice cover periods north of Iceland by Beverton and Lee (1965). There are periods in climatic change lasting about fifty to a hundred years of somewhat irregular occurrence. A recent change in climate has been expressed as a warming of the north-east Atlantic since the late twenties which may have ended in the early sixties of the present century (Bjerknes 1964). A decline in the average strength of the westerlies in the North Atlantic left more residual heat in the water. Towards the European coasts the decline of the westerlies allowed southerly winds to predominate (Dickson, in preparation). Over a long time period the wind direction slowly shifts and the long-term consequence may be that the production cycle shifts away in season from the time of spawning of a fish stock. Equally, a production cycle may shift towards the time of spawning of a fish stock. Fig. 1 shows how a marginal instability in sequence (shown where the variance of recruitment falls below stock at low stock and where it rises above stock at high stock) can lead to the marked reduction or the full expansion of a stock. Such a capacity to respond to environmental change by changes in numbers is the means by which the herring-like fishes survive under adverse conditions. The lack of homeostasis is a primitive character and perhaps the evolutionary step from the primitive herring to the developed cod was the use of growth and hence fecundity to achieve a more powerful mechanism by which the population could be stabilized.

In Fig. 1 are shown the three sources of variation which might affect recruitment, the year to year environmental changes, the larger scale climatic changes and the differences due to stock density. It is possible that all three are mediated by the same processes in food availability during the period of larval drift. A perennial problem facing fisheries biologists is how to distinguish the effects of environmental change on recruitment from those induced by the fishery. The first distinction to be made is between the year to year density independent effects and those associated with large-scale climatic change. The year to year effects, although contributing perhaps a high variance, are considered to be randomly distributed about the stock and recruitment curve and therefore are of no further interest. If the stock and recruitment curve for a given fish species is established independently of the values of recruitment and parent stock then we may consider the curve as given and recruitment as distributed about that curve.

An assumption here is that within an environmental period, recruitment fluctuates randomly and that when the environment changes, recruitment changes markedly and sharply. This concept follows from the supposed homeostatic nature of fecundity, i.e. that the fixed fecundity insulates the stock from minor environmental changes, but allows it to adapt in a favourable or unfavourable manner to major changes.

CONSEQUENCES IN THE REGULATION OF FISHERIES

The more important problem is whether a large scale climatic change has effects on recruitment which can be distinguished from those following a reduction of stock due to fishing. Consider a virgin stock oscillating in time about its replacement point. A failure of recruitment, complete as that in the Plymouth herring (Cushing 1961), would yield a series of points along the abscissa, decreasing in stock as stock fell in consequence. In general, the recruitment/unit stock should decline more quickly with stock than that expected from the stock and recruitment curve. In a stock with a dome-shaped stock and recruitment curve the distinction could perhaps still be made as long as the stock were not too heavily exploited. For herring-like fishes, in which the curve of stock and recruitment is only lightly convex, there would be a real problem of distinction. One would depend upon the difference between the average falling recruitment and that expected about the stock and recruitment curve. If it becomes possible to specify the variance to a stock and recruitment curve, a failing recruitment due to abnormal environmental causes might be distinguishable by ordinary statistical procedures. There is, however, a strong possibility that failure would take place quickly and so there would not be enough information on which to base a judgement. There is, however, a more practical way of achieving the same end. On any stock and recruitment curve there is a point in stock at which recruitment is maximal—Ricker's (1958) point of maximum surplus reproduction at stock P_s with a corresponding exploitation rate E_s. At stock levels below this point, if fishing effort is constant, yield will be reduced and if fishing effort increases at such levels, there is considerable danger that the fishery will be extinguished, if not the stock. There is a limiting exploitation rate, E_1 ($= 1 - e^{-a}$ where $a = P_r/P_m$, P_r is the replacement level of stock and P_m is the level of stock at which maximum recruitment occurs) beyond which the stock is extinguished. If the stock in numbers collapses when the exploitation rate is set at E_s, it must do so through a failure of recruitment due to environmental change. So any stock can be exploited down to the stock level, P_s, at which maximum recruitment is obtainable. Then,

if environmental collapse occurs, the maximum yield has been obtained until the point of collapse.

From a regulatory point of view this means that environmental changes in recruitment can be to some extent ignored. The value P_s can be established from the character of the stock and recruitment curve, i.e. to some extent from the fecundity of the fish. The effect of growth can be taken up in a self-regulatory yield curve of the form proposed but not fully developed by BEVERTON and HOLT (1957). The maximum of such yield curves may tend to lie at stock levels of $P < P_s$, because the exploitation rate E_s may tend to be too high to exploit the benefits of growth to the full. The effect of variance in recruitment about the curve is an important one. In the extreme case of a one-year-class stock under heavy fishing pressure, the variance of stock is essentially the variance of recruitment and so collapse of the fishery could occur near the level of P_s; obviously the variance of the stock is that of the recruitment divided by the number of year-classes.

It might be suggested that if the stock were fished to the maximum sustainable yield on a yield-per-recruit basis, the stock is not vulnerable to recruitment failure through heavy fishing. Fig. 2 (after GULLAND 1967) shows a yield per recruit curve and a yield curve calculated in terms of a stock and recruitment curve. The obvious point is made that the new maximum is at a lower level of stock than that on the yield per recruit curve. But, where yield decreases from the maximum at increasing levels of fishing mortality, and $P < P_s$, the variance of recruitment might generate sufficient variability in stock to endanger it. The danger is greater for the herring-like fishes with a slightly convex stock and recruitment curve than for the cod-like fishes with a curve which is markedly dome-shaped. Indeed the limiting rate of exploitation for herring may occur at levels of fishing mortality hitherto considered as comparatively low.

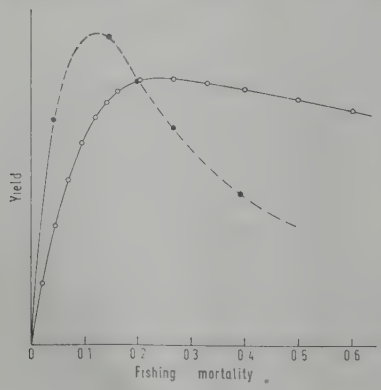

Fig. 2. A yield-per-recruit curve for plaice (full line) and with a stock and recruitment curve (broken line) incorporated (After GULLAND 1967).

The failure of the East Anglian herring stock was one in which $E < E_s$ for a long period during the fifties (Cushing and Bridger 1966) and so the ascription of failure is to fishing. An interesting point is that the fishery took a long time, about a decade, to finally vanish. This was because the variance in recruitment (and hence stock, because during its last decade, it was a one-year-class fishery) was rather low, and because the stock and recruitment curve is only slightly convex. The Arctic cod stock is in danger at the present time, because recruitment has been reduced under pressure of fishing. If we were given the chance to solve the problems of these ancient fisheries again, we should recommend that the stocks be exploited at the best rate of exploitation for the recruitment (either at E_s in numbers, or at the maximum of a self-regulatory yield curve). Then if collapse occurred subsequently through an environmental effect on recruitment, the best yield to that point had been taken. Thus, from the point of view of regulation the environmental factors need not concern us unduly, which is not to say that they should not be predicted.

SUMMARY

There are three sources of variation of recruitment; first that due to random fluctuations alone, secondly that, due to variations in stock and thirdly variations which are extreme at low and high levels of stock and if these occur sequentially can cause catastrophic declines or sharp increases in stock density. From a study of stock/recruitment curves of a number of fish species, it appears that the curve for herring-like fishes differs markedly from those, for example, of cod-like fishes or in more general terms that the shape of the stock/recruitment curve is really a function of its fecundity. That for the herring-like fishes is a near linear curve whereas that for the cod-like fishes is markedly dome-shaped. It follows that the herring-like fishes are very vulnerable to long-term climatic changes and that the cod-like fishes are able to stabilize their populations through long-term climatic changes merely because the increased recruitment when stock is slightly reduced is very much greater than that for the herring-like fishes. If stocks of fish are to be managed then the stock/recruitment relationship has to be taken into account; a form of self regenerating yield curve combining stock/recruitment and yield-per-recruit was in fact put forward by Beverton and Holt. A development of such a curve is needed and one of the uses of such a curve would be that management need not take too much notice of environmental change, because if it occurred the stock would have been exploited at its best rate before any environmental collapse took place.

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FACTORS INFLUENCING YEAR-CLASS STRENGTH OF NORWEGIAN SPRING SPAWNING HERRING (*Clupea harengus* Linné)

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INTRODUCTION

Short and long term variations in abundance of recruits in the Norwegian spring spawning stock of herring (subsequently referred to as Norwegian herring) have been described by several authors (Hjort 1914, Lea 1930, Devold 1963, Marti and Fedorov 1963). Marti (1959) compared the relative strengths of poor and rich year-classes of herring in different areas. For Baltic herring he found a ratio of 1/2–1/3, for North Sea herring, 1/8–1/10 and for Atlanto-Scandian herring, to which the Norwegian herring belong, 1/25–1/30. Lea (1930) estimated the ratio between poor and rich year-classes (with reference to the rich 1904 year-class) in the Norwegian herring stock to be about 1/94. Østvedt (1963) found a ratio of 1/15 for the 1949–1950 year-classes. Thus year-class fluctuations are more pronounced for Norwegian herring than for many other herring stocks in the Northeast Atlantic. Also the time interval between the appearance of rich year-classes can be relatively long, in some periods even more than ten years (Lea 1930, Marti and Fedorov 1963).

The variation in year-class strength in marine fishes is a general phenomenon. The causes of the variation are not known, but the current hypotheses concentrate on possible variability of parental factors (Marti 1959, Bridger 1960, 1961, Cushing and Bridger 1964, Cushing 1968) and of physical and biological conditions in the sea shortly after hatching (Hjort 1914, 1926, Rollefsen 1930, Lea 1930, Walford 1938, 1946, Sette 1943, Carruthers *et al.* 1951, Wiborg 1957). A marked relationship between the number of eggs produced (the spawning potential of the parent stock) and the number of subsequent recruits is demonstrated for some species of fish with low fecundity, e.g. spurdog (*Squalus acanthias* Linné) (Holden 1968). Similarly an indication of such a relationship is found in some relatively small stocks of Pacific herring (*Clupea pallasii* Valenciennes) in British Columbia (Taylor 1963) and in the Downs stock

of herring in the North Sea (Burd and Holford 1968), but no trend of decreasing recruitment with decreasing spawning stock has as yet been demonstrated for the other major stocks of herring in the North Sea (the Buchan and the Bank stocks) and in the Norwegian Sea (the Norwegian herring). However, within the range of population sizes for which data have been available for these stocks, a relationship between the spawning potential of the parent stock and the subsequent year-class strength is difficult to trace due to the variations in the normally high natural mortality rate of the very young stages. Most of the newly hatched larvae die, and slight changes in the mortality rate in the young stages will therefore result in pronounced variations in year-class strength.

Little is known about the causes of the natural mortality rate of the young stages of fish and whether or not there exist periods when the mortality rate is exceptionally high. Hjort (1914, 1926) expounded the concept of a critical period at the end of the yolk sac stage when the larvae begin feeding. Experiments carried out on herring (Soleim 1942) indicated that a critical period existed at this stage. Thus the natural conditions during the early stages of the life might determine the abundance of herring entering the exploited stock and the variations in spawning potential and its influence on subsequent year-class strength might be of minor importance when the size of the spawning stock is above a certain level.

In view of the serious decline in the yield of adult Norwegian herring during the late 1950s and early 1960s the Herring Committee of the International Council for the Exploration of the Sea (ICES) recommended that special attention should be given to the recruitment problem in this stock (Parrish 1963). At the Institute of Marine Research, Bergen, investigations of the variation in size of the spawning stock, the location and time of spawning, the identification of possible critical stages during the early larval development and the larval drift have been emphasized. During the same period extensive investigations were conducted to register the distribution, migration, abundance and mortality of young and adolescent herring. The results of the latter investigations are presented in a separate paper (Dragesund 1970) while this account is confined to:

1) spawning characteristics, i.e. the structure and size of the spawning stock and the location and time of spawning;
2) larval studies during the first month after hatching.

The discussion is centred on year-class fluctuations in relation to spawning characteristics and to environmental conditions during the egg stage and early larval development.

MATERIAL AND METHODS

The major part of the material is related to the 1959–1965 year-classes, and the data are mainly obtained from:

1) samples of herring collected during the Norwegian winter herring fisheries in 1959–1968;
2) tagging experiments carried out in 1952–1964;
3) samples of herring larvae collected in 1959–1965 and in 1968;
4) larval drift experiments;
5) official fishery statistics and meteorological annals.

When it is of importance to extend the information to other year-classes, data from the literature and unpublished data from the records of the Institute of Marine Research, Bergen, are used.

The statistical methods applied are those given in text books of statistical analysis (Snedecor 1956, Godske 1966). Geographical names or area code numbers used in the text are shown in Fig. 1. The hydrographical data are from the records of the Institute of Marine Research, Bergen.

ADULT HERRING

Samples of adult herring, each usually consisting of 100 specimens, were collected from commercial catches several times each week during the Norwegian winter herring fishery. Fresh or iced material was brought to the laboratory for examination. Until January 1963 lengths were measured to the nearest half cm and after this date to the half cm below as recommended by ICES (Anon. 1963). To make the data comparable a correction factor of 0.25 cm has been added to the mean lengths of herring in samples collected after January 1963. Ages were determined from scale readings. The weight in g was recorded, and the maturity stages were classified according to the scale recommended by ICES (Anon. 1963). This maturity scale comprises eight stages including six which describe the sexual cycle of adult fish, i.e. stages III–VIII. The stages V–VII represent the pre-spawning, the spawning and the spent phases, respectively.

Stage V. Gonads fill body cavity. Eggs large, round, some are transparent. Ovaries yellowish, testes milk white. Sperm does not flow, but can be extruded by pressure.

Stage VI. Eggs transparent. Testes white. Eggs and sperm flow freely.

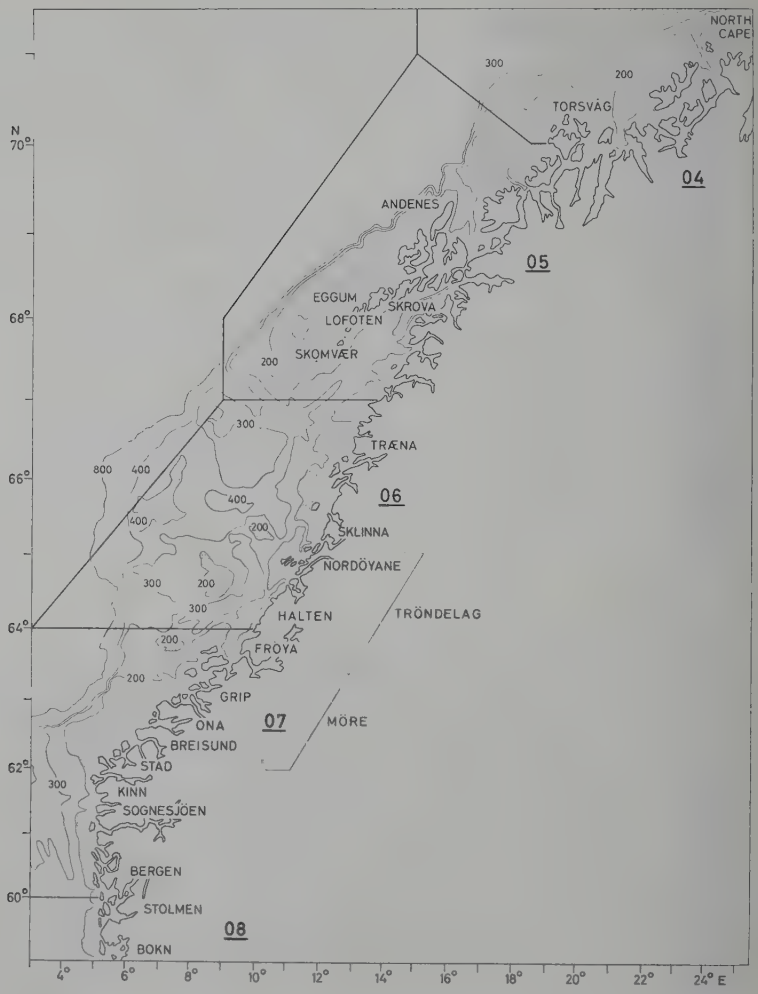


Fig. 1. Names and code numbers of areas mentioned in the text, and general bathymetric features of the coastal banks (depths in m).

Stage VII. Gonads baggy, bloodshot. The ovaries empty or containing only a few residual eggs. Testes may contain remains of sperm.

The biological data dealt with are from annual reports published by Østvedt (1961, 1962, 1965, 1966), Devold and Østvedt (1963, 1964) and Dragesund (1967, 1968a, 1968b) and from unpublished records available at the Institute of Marine Research, Bergen. Statistical information on the Norwegian landings was obtained from annual reports on the Norwegian herring fisheries (Anon. 1960–1966a). The method used to estimate the adult stock size has been described by Dragesund and Jakobsson (1963), where estimates for the period 1952–1959 are also given. For the years 1964 and 1965 unpublished data are available at the Institute of Marine Research, Bergen, and the Fisheries Research Institute, Reykjavik.

LARVAL HERRING

The larvae were collected on surveys covering the Norwegian coastal banks from Stad to Lofoten (Wiborg 1960, 1961, 1962a, 1962b, Dragesund and Wiborg 1963, Dragesund 1965, Dragesund and Hognestad 1966). The area was usually surveyed twice and the sampling was carried out from south to north and south again with one research vessel. Oblique hauls were taken with Clarke–Bumpus plankton samplers (CBPS) with a tube aperture of 13 cm diameter (Clarke and Bumpus 1950). The length of the nylon or silk nets used was 60 cm with a mesh size of 0.50 mm. The CBPS were equipped with flowmeters and two samplers were towed simultaneously at different depths and raised in 5 m steps. The sampling depths were 25–5 m, 50–30 m, and occasionally 75–55 m. The total towing time was 20 minutes. A weight of 28 kg was attached at the end of the 4 mm thick wire, which was kept as close as possible to an angle of 50° from the surface by keeping the towing speed between 1.5 and 2.0 knots.

Because of difficulties in operating the closing mechanism of the CBPS in bad weather, this was permanently kept in an open position. The bias caused by this is considered to be of little importance, except when larval density in the uppermost depth interval is high compared with the depth intervals below.

In 1959 sampling with CBPS was carried out during a relatively late period (20–28 April) in the second part of the survey only. However, larvae were collected during the entire 1959 survey in vertical hauls from the bottom to the surface with a 1 m diameter Nansen net (Nansen 1915). Sampling with Isaacs–Kidd three-foot midwater trawl (IKMT) (Aron 1962) was made at selected stations during the 1964 survey.

The larvae were preserved in diluted formalin containing 4% formal dehyde. At the laboratory they were counted and measured to the neares mm below and classified as larvae with or without yolk sac. According t Blaxter (1968) herring larvae shrink about 12% in length in a fixativ of the type used. The shrinkage of the larvae was not taken into accoun when working out the length distributions, but since the larvae wer preserved and measured in the same way each year the length distribu tions are assumed to be comparable from year to year.

To facilitate comparison between stations and from year to year, th number of larvae collected with CBPS was converted to numbers belo 1 m^2 of surface by multiplying the original numbers for each station wit the sampling interval and then dividing by the water volume filtered. Fo analysis of vertical distribution the number of larvae per 1 m^3 water wa calculated. The number of larvae collected with the Nansen net wa converted to numbers below 1 m^2 of surface by dividing the number o larvae caught by the area (in m^2) of the net aperture. The abundanc estimates obtained by CBPS and Nansen net are not comparable.

LARVAL DRIFT

Freely floating drogues were used at several localities in 1964 an 1965 in order to study the drifting velocity of larvae. The drogue wa made of two iron sheets having the dimensions of $0.2 \times 100 \times 100$ cm an fixed at right angles to each other. The drogue was suspended by a 1.6 mm thick nylon line from a plastic float to which a pole was attached. Th pole was equipped with a light on the top, about 2 m above the surface The positions of the drogues were determined by Loran and radar. I addition the larval drift pattern was deduced from wind observations an drift bottle experiments.

The wind data are from the meteorological stations Ona (N 62° 54 E 06° 30.5′), Nordøyane (N 64° 48′, E 10° 33′) and Skomvær (N 67° 25 E 11° 53′) as reported in Norsk Meteorologisk Årbok (Anon. 1960–1966b) Wind forces are given in Beaufort units and wind directions in twelv sectors, each covering 30°. The wind observations were transformed int monthly wind vectors. These were obtained by multiplying for eac direction and month the mean wind force with the frequencies of observa tions of wind in the particular direction and thereafter the resultan vector was constructed from those established for each direction.

In 1961, 1963, 1964 and 1965 drift bottles were released in larva patches at various places along the coast. The bottles had an inne volume of 350 ml and weighed 530 g. A letter inside each bottle requeste the finder to report the date and place of recovery.

EVALUATION OF FACTORS AFFECTING LARVAL ABUNDANCE ESTIMATES

Several methods have been employed to estimate the annual abundance of planktonic fish eggs and larvae (e.g. BUCHANAN-WOLLASTON 1926, SETTE and AHLSTROM 1948, TAFT 1960, SAVILLE 1963). ENGLISH (1963) analysed some common procedures of estimating annual abundance of planktonic fish eggs. The data used were treated by analysis of variance and he concluded that the major source of variability in estimates of annual egg abundance is the time effect. This is mainly due to the unknown fluctuations in time and location of maximum egg abundance. The number of stations was less important and duplications (paired hauls) were least important.

Reliable estimates of annual abundance of larvae are more difficult to obtain than for planktonic eggs, especially because of net avoidance and variation in diurnal behaviour of the larvae. In the present work, therefore, no attempt will be made to estimate the total abundance of herring larvae at hatching or at subsequent stages. The low number of surveys (usually two per season) and the long distance between stations (about ten nautical miles) do not allow for such estimates. Moreover, the sampling time was not always the same relative to the time of spawning. The numerical values obtained, therefore, are used only to show trends in the geographical distribution and to give some estimates of larval abundance at selected sections. The distribution charts were made by plotting the figures for each station and drawing isolines of abundance.

The haul-to-haul variation in oblique hauls with CBPS was investigated at some stations during the 1964 survey by comparing the number of larvae caught:

1) at the same station in two subsequent hauls (Table I);
2) in two samplers attached above each other, 1 m apart (Table II).

An analysis of variance was applied to these data using a log-transformation, log (x+k), where x is the number of larvae below 1 m^2 of surface and k=1 (CASSIE 1968). The calculations (Tables 1 and 2) show that

Table 1. Analysis of variance of the data in Table I.

Source of variation	Sums of squares	Degrees of freedom	Variance of estimate	Value of F	Probability
Between series of haul	0.036	1	0.036		
Between hauls	7.675	15	0.512		
"Residual"	0.806	15	0.054	0.667	>0.05
Total	8.517	31			

Table 2. Analysis of variance of the data in Table II.

Source of variation	Sums of squares	Degrees of freedom	Variance of estimate	Value of F	Probability
Between series of haul	0.004	1	0.004		
Between hauls	17.471	20	0.874		
"Residual"	0.628	20	0.031	0.129	>0.05
Total	18.103	41			

there was no significant difference ($P > 0.05$) in numbers between series of hauls or between catches from approximately the same depth. The results from this analysis indicated that the larvae were evenly distributed within the relatively small area sampled. The error caused by the variability in catch of replicate hauls in the same body of water is therefore assumed to be relatively small compared with that introduced by taking a sample over a small area as being representative of a much larger area.

Knowledge of the avoidance of sampling devices by planktonic organisms (including fish larvae) has been reviewed by CLUTTER and ANRAKU (1968). Even if the results are contradictory the accumulated data indicate that avoidance occurs. They reported that the catching efficiency increases with increasing speed of the net, and that larger fish larvae avoid nets towed at low speed to a greater extent than do the smaller larvae. It is assumed, therefore, that CBPS being towed at 1.5–2.0 knots will catch the fish larvae less efficiently than will high speed samplers, e.g. the Gulf III (GEHRINGER 1952).

In order to evaluate the effect of avoidance by herring larvae for CBPS, comparisons were made of the length distributions of larvae caught with IKMT and CBPS. Moreover, comparisons were made of the length distributions in catches taken by CBPS around subsurface drogues at night and during the day. The IKMT generally caught larger larvae than the CBPS (Table 3). However, no significant difference in mean length was found for the smallest larvae. Larger larvae were caught at night at drift stations 2 and 5 (off Sklinna and Frøya), whereas at drift station 4 (off Eggum) they occurred in the samples during the daytime (Table 4).

The diurnal variation in catches was analysed by sampling larvae at different depth layers around subsurface drogues every second hour during a 24-hour period at the three mentioned drift stations (Table III). At station 2 (off Sklinna) the number of larvae caught at night was significantly higher than at daytime ($P < 0.05$), whereas at stations 4 and 5 (off Eggum and Frøya) no significant difference was found (Table 5).

Although the results are somewhat ambiguous it is assumed that the net avoidance will affect both length distributions and abundance esti-

Table 3. Comparison between mean lengths ($\bar{l}$) of larvae caught with IKMT and CBPS during the 1964 survey.

Locality	Date	Hour	Gear	Depth in m	No. of larvae	$\bar{l}$ in mm	Standard deviation	Value of Student's t	Probability
Off Halten	16.4	1724–1910	IKMT	25–5	7	12.7	1.20	0.362	>0.05
			CBPS	25–5	7	12.4	1.84		
Off Sklinna	18–19.4	1920–1540	IKMT	50–30	113	14.9	1.97	0.746	>0.05
			CBPS	50–30	16	15.3	2.26		
Off Eggum	28–29.4	1455–0910	IKMT	50–30	84	12.2	2.26	0.152	>0.05
			CBPS	50–30	334	12.1	1.53		
Off Træna	1.5	0145	IKMT	50–30	159	18.2	1.95	8.257	<0.05
		0105	CBPS	50–30	27	14.7	3.74		
		0558–0820	IKMT	50–30	90	17.2	2.43	4.380	<0.05
		0524–0741	CBPS	50–30	16	14.2	3.03		
Off Sklinna	2.5	0227	IKMT	50–30	42	18.7	2.18	4.632	<0.05
		0150	CBPS	50–30	30	14.9	4.66		
Off Halten	3.5	0228	IKMT	50–30	63	21.1	1.65	3,717	<0.05
		0150	CBPS	50–30	5	18.0	3.32		
		1047	IKMT	50–30	23	16.3	2.21	0.455	>0.05
		1055	CBPS	50–30	3	15.7	1.25		
Off Grip	4.5	0543	IKMT	50–30	1	19.0	—		
		0343	CBPS	50–30	4	14.3	2.94		

Table 4. Comparison between mean lengths ($\bar{l}$) of larvae caught by night and by day in obli hauls from 50 to 5 m with CBPS at three drift stations.

Drift station no.	Date	Time	No. of larvae	$\bar{l}$ in mm	Standard deviation	Value of Student's t	Probabili
2	1964 18–19.4	Night	244	16.1	1.95	1.983	<0.05
		Day	94	15.6	2.37		
4	1964 28–29.4	Night	505	12.0	1.54	2.494	<0.05
		Day	1275	12.2	1.52		
5	1965 9–10.4	Night	157	12.2	1.49	5.359	<0.05
		Day	271	11.5	1.18		

Table 5. Analysis of variance of the data in Table III. The calculations were made on the $(x+1)$ transformation.

Drift station no.	Source of variation	Sums of squares	Degrees of freedom	Variance of estimate	Value of F	Probabili
2	Between day and night	1.468	1	1.468		
	Within day and night	1.570	11	0.143	10.290	<0.05
	Total	3.038	12			
4	Between day and night	0.015	1	0.015		
	Within day and night	0.192	11	0.017	0.882	>0.05
	Total	0.207	12			
5	Between day and night	0.284	1	0.284		
	Within day and night	0.851	10	0.085	3.341	>0.05
	Total	1.135	11			

mates, especially when the larvae are longer than 15 mm. However, since there was no clear diurnal variation in the catches, it was not considered necessary to apply any conversion factor to make catches comparable to those taken by night.

During the 1959 and 1960 surveys sampling with CBPS was carried out only from 25 to 5 m, and to make the catches comparable with the following years a conversion factor was estimated and used to compensate for the lack of sampling in 50–30 m. The number of larvae caught at each station during the 1959 and 1960 surveys at depths of 25–5 m was multiplied by a factor of 1.7, which is the ratio between the number of larvae

caught at 50–5 m and 25–5 m, respectively, during the cruises in 1961–1965. Larvae also occur below 50 m and the larval abundance is, therefore, underestimated by the present sampling procedure. However, samples are scarce from depths below 50 m, and no attempt has been made to compensate for this underestimate.

SPAWNING CHARACTERISTICS

SPAWNING STOCK

During the period 1959–1962 the spawning stock had only one component which migrated towards the coast off Møre (area 07) from the usual wintering area east of Iceland (Devold 1963). The major part of the stock again approached the coast from this wintering area in 1963–1965, but a second component migrated towards the Lofoten region (area 05) from another wintering area, located off the coast between Torsvåg and North Cape (Devold 1968). The herring arrived off Møre at the end of January and during February. The other component reached the Lofoten spawning grounds three to four weeks later, except in 1965.

In 1959–1963 the rich 1950 year-class dominated in the spawning stock off Møre (Table 6). In 1963 the age structure of the stock changed as recruit spawners from the 1959 year-class appeared in the catches. In 1964 and 1965 this year-class dominated in the spawning stock both off Møre (area 07) and at Lofoten (area 05), but herring of the 1960 and the 1961 year-classes were also present on the spawning grounds. In 1965 these three year-classes made up 80–85% of the total catches off Møre. The spawning stock at Lofoten consisted almost entirely of the 1959–1961 year-classes.

In 1959 recruit spawners constituted 11.7% of the herring caught off Møre and 21.3% of those caught between Bokn and Stolmen (Table 7). During the seasons in 1960–1963 the percentage of recruit spawners was considerably lower, except in 1963 at Lofoten where only recruit spawners were recorded. In 1964 and 1965 recruit spawners made up 34.4% and 35.9% respectively of the herring off Møre with the corresponding percentages for the Lofoten region being 93.7% and 76.4%.

Estimates of the absolute size of the spawning stock based on tagging experiments are available for the years 1952–1959 and 1964–1965 (Dragesund and Jakobsson 1963, Anon. 1969). Estimates obtained from combined acoustic surveys and underwater photography experiments for the years 1959 and 1962–1965 are also available (Fedorov, Truskanov and Yudanov 1963, Anon. 1969). The results are illustrated in Fig. 2. The average figures are given for years when both methods have been used.

Table 6. Age composition (in %) of Norwegian herring caught with purse seine during the spawning seasons in 1959–1968.

Year	Area	Total no.	Year-class														Mean age
			1963	1962	1961	1960	1959	1958	1957	1956	1955	1954	1953	1952	1951	1950	<1950	
1959	08	553						—	—	0.4	1.3	4.0	17.4	6.0	8.0	51.8	11.1	8.4
	07	2106						—	—	—	0.7	1.1	7.1	5.7	8.4	54.1	22.9	9.5
	06	94						—	—	—	—	—	2.1	3.2	4.2	73.4	17.1	9.5
1960	07	3038					—	—	—	0.2	1.4	1.2	6.1	3.6	5.3	64.4	17.8	10.3
1961	07	666				—	—	—	0.4	0.9	3.3	2.9	7.7	4.8	6.5	59.0	14.5	10.7
1962	07	992			—	—	0.1	—	0.5	1.0	2.7	1.5	7.8	4.2	6.6	62.7	12.9	11.7
	06	80			—	—	—	—	—	—	—	1.3	11.2	2.5	7.5	73.7	3.8	11.7
1963	07	923		—	—	—	4.0	0.3	0.4	0.7	1.8	1.7	8.7	3.6	8.3	61.1	9.4	12.2
	06	314		—	—	—	13.1	0.3	—	—	—	0.3	7.3	3.2	7.3	62.5	6.0	11.6
	05	433		—	—	9.5	89.8	0.7	—	—	—	—	—	—	—	—	—	3.9
1964	07	1198	—	—	—	4.0	51.5	0.4	0.2	0.7	1.3	0.5	4.2	2.2	3.2	28.0	3.8	8.7
	05	1089	—	—	0.6	10.1	88.4	0.3	—	—	—	—	0.1	—	—	0.5	—	4.9
1965	07	1141	—	—	3.2	10.7	62.7	0.1	0.2	—	0.4	0.9	2.0	1.4	2.2	14.4	1.8	7.8
	06	96	—	—	18.8	26.0	55.2	—	—	—	—	—	—	—	—	—	—	5.4
	05	719	—	—	5.8	19.6	74.1	0.1	—	—	—	—	0.3	—	—	—	0.1	5.7
1966	07	2963	—	0.1	10.3	27.7	53.4	0.2	0.2	0.1	0.2	0.3	0.7	0.7	0.4	5.2	0.5	7.2
	06	471	—	—	3.6	25.1	60.8	—	—	0.2	—	—	0.6	0.6	0.2	8.5	0.4	7.6
	05	749	—	0.3	8.0	39.1	51.6	0.3	—	—	—	—	—	0.1	0.3	0.3	—	6.5
1967	07	2135	0.5	0.4	13.4	32.1	48.8	0.1	0.1	0.1	0.2	0.3	0.7	0.3	0.3	2.6	0.1	7.3
	06	99	1.0	—	10.1	41.4	46.5	1.0	—	—	—	—	—	—	—	—	—	7.4
1968	07	1352	0.7	1.7	13.8	34.2	46.9	0.2	—	0.1	0.2	0.2	0.7	0.3	—	1.0	—	8.5
	06	243	0.8	1.2	9.9	34.6	51.5	—	—	—	—	—	0.4	—	—	1.2	0.4	8.6

Table 7. Composition (in %) of recruit and repeat spawners of Norwegian herring during the spawning seasons in 1959–1965.

Year	Area	Region	No.	Recruit spawners	Repeat spawners
1959	08	Bokn-Stolmen	816	21.3	78.7
1959	07	Stad-Frøya	1761	11.7	88.3
1960	07	Stad-Frøya	3991	3.9	96.1
1961	07	Stad-Frøya	2610	1.0	99.0
1962	07	Stad-Frøya	2842	0.5	99.5
1963	07	Stad-Frøya	1938	5.2	94.8
1963	05	Off Lofoten	434	100.0	—
1964	07	Ona-Frøya	2097	34.4	65.6
1964	05	Off Lofoten	1176	93.7	6.3
1965	07	Ona-Grip	1270	35.9	64.1
1965	06	Off Halten	96	87.5	12.5
1965	05	Off Lofoten	643	76.4	23.6

The stock estimates for the 1952–1965 period vary between 2.5 and 20.0 million tons with the highest figures for 1952–1956. From 1957 onwards a rapid decrease in the stock took place and this continued until 1962 when it was about 2.5 million tons. In the following three years the stock increased from 2.9 million tons in 1963 to 7.3 million tons in 1965

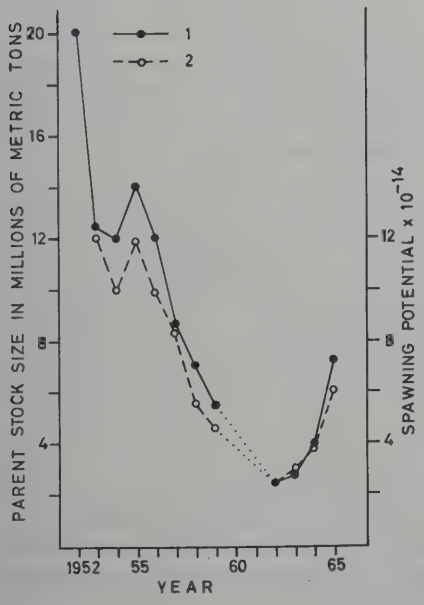


Fig. 2. Variation in, (1) parent stock size of Norwegian herring during the spawning seasons in 1952–1965 and (2) number of eggs spawned (spawning potential).

due to recruitment from the rich 1959 year-class. The estimates for 1963–1965 do not include the component spawning off Lofoten, and the total spawning stock in these years, therefore, is underestimated. Abundance indices obtained from data on catch per unit effort (Østvedt 1963) indicated that the estimate of the stock size for 1952 is too high. The figures for the period 1953–1959 follow the same trend as the abundance indices given by Østvedt.

The spawning potential of the stock is positively correlated to the size of the stock. However, fecundity (the number of eggs in the gonads of individual fish) increases with length and weight of the fish, and thus the spawning potential of the stock is a function both of the number and the length distribution of fish. In order to analyse the year by year variations of the spawning potential, the stock size in tons in the different years were converted to numbers of fish by length. Length and weight data of herring collected from purse seine catches were used to give stock estimates in tons for the different length groups. The estimated stock sizes in weight by length were then divided by the corresponding mean weight of herring in each length group. The sex ratio of spawning Norwegian herring is approximately 1:1 (Dragesund unpublished). With data on fecundity by length (Parrish and Saville 1965), the number of eggs deposited each year, therefore, could be calculated (Fig. 2). The variations in the spawning potential follow the same trend as that of the stock estimates in tons. However, in years when young individuals dominated in the spawning stock, as in 1954–1956 (Østvedt 1963) and in 1964–1965, the spawning potential was relatively low compared to years when the stock consisted of old individuals, as in 1962–1963.

The following characteristic features concerning the structure and size of the spawning stock during the period 1959–1965 can be listed:

1) the mean age of the stock increased from 1959 to 1963 with the 1950 year-class predominating;
2) the 1959 year-class dominated in the stock in 1964 and 1965 and the percentage of recruit spawners was highest these years;
3) the stock size had its lowest values in 1961–1963 and its highest in 1965;
4) the stock size was on a considerably lower level in 1959–1965 than in the mid 1950s.

LOCATION AND TIME OF SPAWNING

The spawning grounds were located by studying the geographical distribution of catches of spawning and spent herring and by surveying the coastal banks for newly hatched larvae. Herring remain on the same

grounds from just before spawning until they gradually migrate from the coastal banks. The distribution of catches during the spawning season, therefore, will give information on the location of spawning (Fig. 3). The occurrence of larvae with yolk sac indicates that spawning must have taken place not very far from the locality of capture. The distribution of yolk sac larvae coincided fairly well with the distribution of catches of spawning and spent herring (Fig. 3). However, in some years the larvae were found distributed slightly to the west and north of the herring catches. This could be expected since the yolk sac stage lasts for some days, about ten days at 8°C (Blaxter and Hempel 1963), and a dispersion from the spawning grounds evidently takes place during this time. In 1964 the survey was made late in relation to the main spawning season, and therefore only few yolk sac larvae were found in areas 07 and 06 that year.

Although the data are insufficient for a precise determination of the spawning grounds, it can be concluded that spawning was concentrated within four following areas:

1) area 08, between Bokn and Stolmen;
2) area 07, between Kinn and Frøya;
3) area 06, between Halten and Sklinna;
4) area 05, off the Lofoten Islands.

During the period 1959–1965 the most important spawning took place in area 07. In 1959–1962 the majority of the herring in this area tended to concentrate somewhat farther south (between Stad and Ona) than in 1963–1965, when the centre of spawning was located between Ona and Grip. Spawning in area 08 was negligible except in 1959 when spawning was observed at certain places along the coast as far south as Bokn. The spawning between Halten and Sklinna (area 06) occurred regularly and did not show any change in location. Mass spawning off the Lofoten Islands (area 05) was not recorded during the period 1959–1962. However, a few yolk sac larvae caught in this region in 1960 suggest spawning there that year. From 1963 to 1965 herring spawned regularly at Lofoten.

The distribution of relative catches of spawning and spent herring presumably give the best indication of the geographical distribution of the spawning area. In Table 8 the number of rectangles shown in Fig. 3 in which spawning and spent herring were caught, is listed. For 1960 and 1961, within area 06, the distribution of yolk sac larvae was used. The spawning was restricted to grounds with sandy or rocky bottom, and not all the grounds within the rectangles shown in Fig. 3 constitute localities for spawning. Within the two southern spawning areas (08 and 07) a restriction in the geographical distribution of the catches were found from

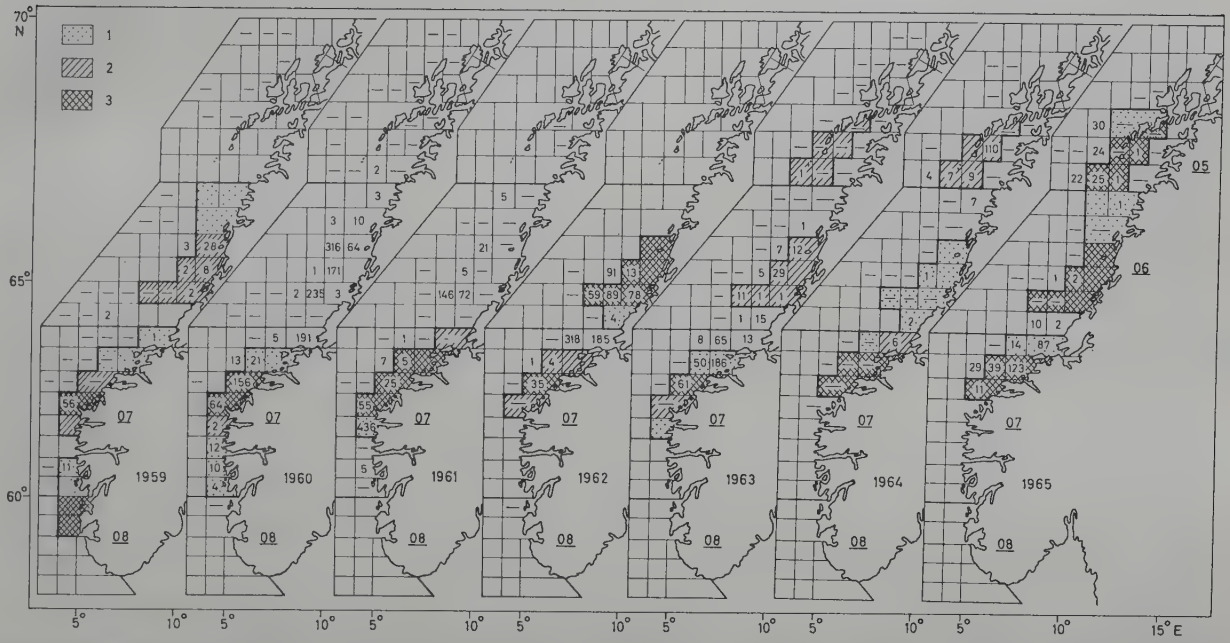


Fig. 3. Distribution of relative catches of spawning and spent herring during the Norwegian winter herring seasons in 1959–1965. Legend: (1) <5%, (2) 5–15% and (3) >15% of the total catches, respectively. The figures in the rectangles denote numbers of yolk sac larvae per station below 1 m² of surface. The horizontal lines denote hauls without larvae.

1959 to 1965, accompanied with an increase in the extension within area 05 from 1963 to 1965. The extension of the spawning area seemed to decrease with the size of the spawning stock, being most restricted in 1961 and 1962.

Table 8. Extension of spawning area indicated by number of rectangles shown in Fig. 3 in which spawning and spent herring were caught in 1959–1965.

Area	Spawning year						
	1959	1960	1961	1962	1963	1964	1965
08	2	0	0	0	0	0	0
07	8	8	6	4	5	5	5
06	9	9?	5?	7	6	7	9
05	?	?	?	?	5	5	6

Even in the same locality groups of herring which keep together will spawn at slightly different times. The time of the main spawning is estimated from the composition of the various maturity stages of herring in samples collected just prior to and during the spawning season. The duration of the spawning season is defined as the time between the first and last occurrence of herring in stage VII.

In Fig. 4 the relative frequency for the different maturity stages is plotted against time (in five-day periods). The data used in the figure are listed in Table IV. The time when the first fish were found in maturity stage VII, indicating the commencement of spawning (T_1), could be determined fairly accurately, but the time for the end of spawning (T_2) was more difficult to assess from the present material since some herring in stage V occurred in samples collected even at the end of the sampling period. These herring had to pass through stage VI before the season could be considered ended. The duration of stage VI for the individual fish is incompletely known for Norwegian herring, but this stage is the shortest (Iles 1964). To get approximate figures for the duration of stage VI, the time interval between the first occurrence of stages VII and VI (T_d) was measured. By adding T_d to the last time when herring in maturity stage V occurred, the end of the spawning season (T_2) was estimated. The time of the main spawning is defined to occur at the mid-point between T_1 and T_2 (Fig. 4).

In area 07 (off Møre) spawning commenced relatively early in 1959, 1960 and 1965, when the main spawning took place in the first week of March. In 1962 and 1963 the onset of spawning was late and the main spawning occurred 15–19 and 10–14 March, respectively. The duration of the spawning seasons in 1959–1965 was longest in 1959, 1960 and 1961,

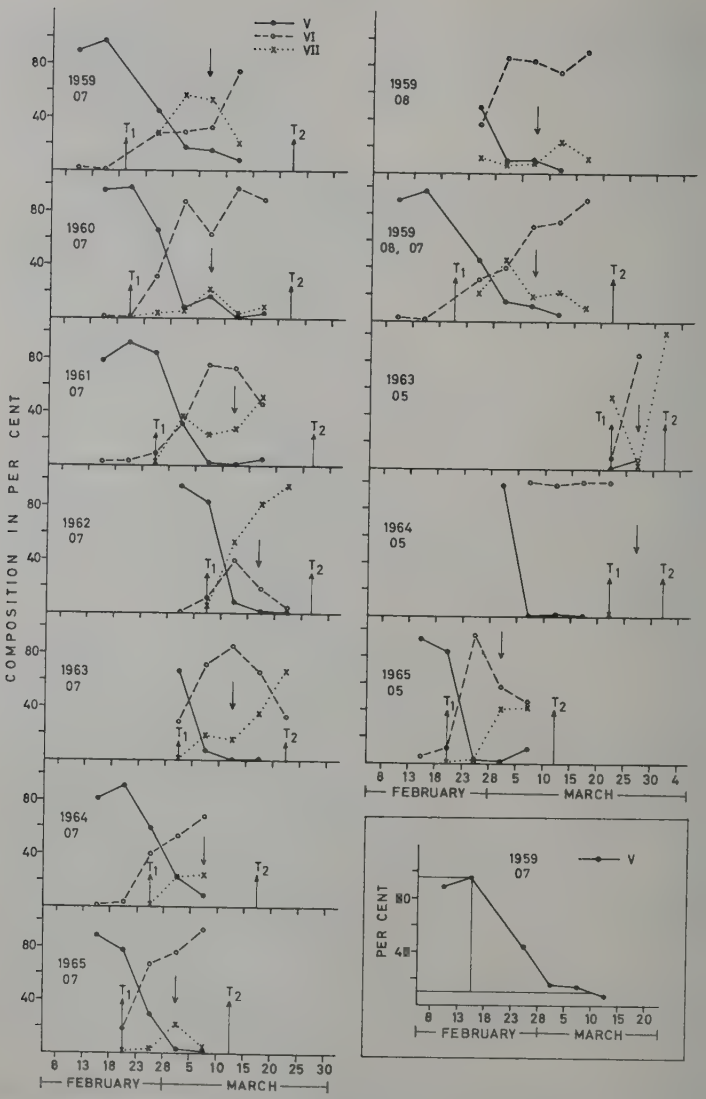


Fig. 4. Maturity composition (in %) of stages V–VII in samples of Norwegian herring collected during the spawning seasons in 1959–1965. Data for males and females are pooled and plotted against time in five-day periods. T_1 and T_2 represent the onset and end of spawning. The time of main spawning is indicated as the midpoint between T_1 and T_2 by an unlabelled arrow. The inserted illustration of the method used to estimate the spawning rate by measuring the reduction of stage V is explained in the text.

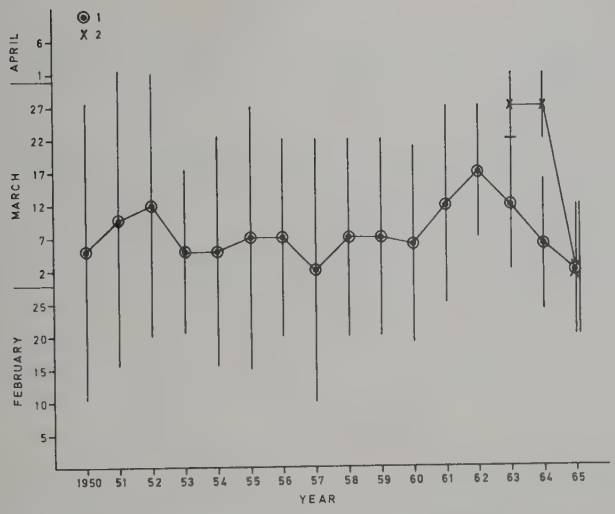


Fig. 5. Time of main spawning during the period 1950–1965, (1) within areas 07 and 08 and (2) within area 05. Vertical bars denote duration of the spawning season.

lasting for about one month. In the other years the season lasted only about three weeks.

In area 06 (between Halten and Sklinna) the duration of spawning in 1959 could not be studied in the same detail because of the limited number of samples available. Apparently, spawning occurred almost at the same time or slightly later than in area 07. Herring examined from the Halten Bank showed that spawning commenced a few days later there than elsewhere in area 06. In area 05 (off Lofoten) the onset of spawning was late in 1963 as well as in 1964, and lasted only about ten days. In 1965 the onset and duration of spawning were the same as in area 07.

In Fig. 5 the time of the main spawning and the duration of the spawning season are illustrated for the period 1959–1965, supplemented with data from the spawning seasons in 1950–1958. No special trend in time of the main spawning was found during the period 1950–1965. However, the spawning seasons lasted somewhat longer in 1950–1958 than during the period 1959–1965, probably because of the restricted spawning in the southernmost region within area 08.

In the spawning seasons of 1964 and 1965 the influx of recruits was high. A comparison between the onset of spawning for recruit and repeat spawners these years is given in Table 9. Apparently no marked difference

Table 9. Composition (in %) of the maturity stages of Norwegian herring in five-day periods during the spawning season in 1964 and 1965.

Area	Date		Recruit spawners					Repeat spawners				
			No.	Maturity stage				No.	Maturity stage			
				IV	V	VI	VII		IV	V	VI	VII
07	1964	13–17.2	137	20.4	78.8	0.8	—	228	17.1	82.9	—	—
		18–22.2	223	9.0	87.0	4.0	—	238	0.8	95.4	3.8	—
		23–27.2	208	1.4	57.7	39.4	1.5	428	0.2	59.6	39.7	0.5
		28.2–3.3	83	1.2	26.5	54.2	18.1	237	0.4	21.2	52.7	25.7
		4–8.3	71	—	14.1	71.8	14.1	224	—	7.4	65.6	27.0
05	1964	28.2–3.3	79	2.5	97.5	—	—	3	—	100.0	—	—
		4–8.3	80	—	—	100.0	—	14	—	—	100.0	—
		9–13.3	92	—	2.2	97.8	—	3	—	—	100.0	—
		14–18.3	513	—	0.2	99.8	—	27	—	—	100.0	—
		19–23.3	338	—	—	99.1	0.9	27	—	—	100.0	—
07	1965	13–17.2	115	26.1	73.9	—	—	202	3.0	97.0	—	—
		18–22.2	146	9.6	72.6	17.8	—	258	—	79.8	19.8	0.4
		23–27.2	45	2.2	33.3	57.8	6.7	203	—	29.0	68.0	3.0
		28.2–4.3	110	1.8	1.8	63.6	32.8	95	—	5.3	88.4	6.3
		5–9.3	40	—	2.5	95.0	2.5	56	—	—	92.9	7.1
06	1965	15–19.3	84	—	—	92.9	7.1	12	—	—	100.0	—
05	1965	13–17.2	70	2.9	91.4	5.7	—	25	—	96.0	4.0	—
		18–22.2	129	5.4	86.0	7.8	0.8	46	2.2	76.1	21.7	—
		23–27.2	71	—	2.8	94.4	2.8	23	—	—	100.0	—
		28.2–4.3	142	—	2.2	57.0	40.8	45	—	—	60.0	40.0
		5–9.3	79	1.3	12.7	49.6	36.4	13	—	—	30.8	69.2

was found in the onset of spawning although repeat spawners reached maturity stages VI and VII a little earlier than the recruits. This suggests that recruits spawned slightly later than the repeat spawners, especially in area 07.

The transition from the prespawning to the spawning stage was studied by estimating the rate of reduction for the maturity stage V from the maximum frequency points of the stage V curves to their 10% levels. The percentage reduction was measured (Fig. 4) and the reduction per day (defined as the spawning rate) was estimated (Table 10). The figure for 1962 (area 07) indicates mass spawning over a relatively short period, whereas in 1959 spawning took place at a considerably slower rate. The spawning in the other years occurred at a more moderate rate than in 1962. In area 05 (off Lofoten) the spawning rate was generally higher than in area 07 (off Møre), especially in 1964.

Table 10. Spawning rate of Norwegian herring indicated by the percentage reduction of the maturity stage V per day (see text for explanation).

Area	Spawning year						
	1959	1960	1961	1962	1963	1964	1965
07	3.8	5.9	6.3	8.7	—	5.3	5.3
05	—	—	—	—	—	22.0	10.3

TIME OF HATCHING

The time of main hatching can be found by adding the incubation period to the time of main spawning. Knowing the temperature on the spawning grounds, an approximate figure for the incubation period can be estimated (Blaxter and Hempel 1963). The incubation period varies from about twenty-five days at 5 °C to about sixteen days at 8 °C. Investigations carried out off Møre (unpublished) during the spawning seasons in 1967 and 1968, showed that the spawning took place at depths less than 250 m, with the most frequent spawning depths ranging from 50 to 200 m. Therefore, the mean temperature between 50 and 200 m (or bottom) in the different regions was used in order to estimate the incubation period (Fig. 6). The stations were located on the main spawning grounds within each region. The number of stations varied between two and four. The mean temperature in the spawning region off Møre (area 07) was lowest in 1959 and 1963 resulting in a correspondingly longer incubation period than in the other years. The quartile intervals, indicat-

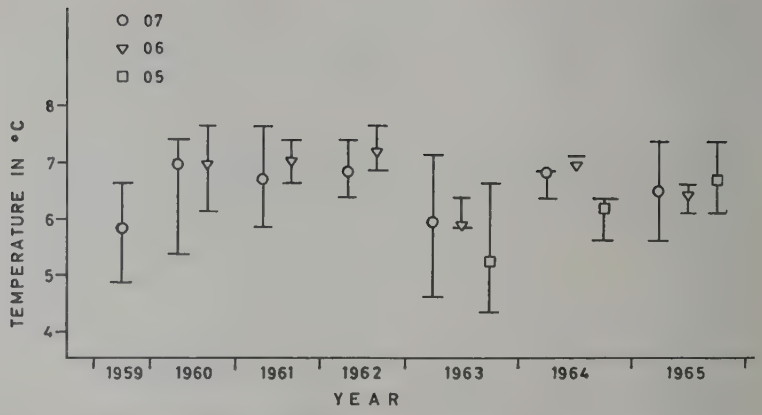
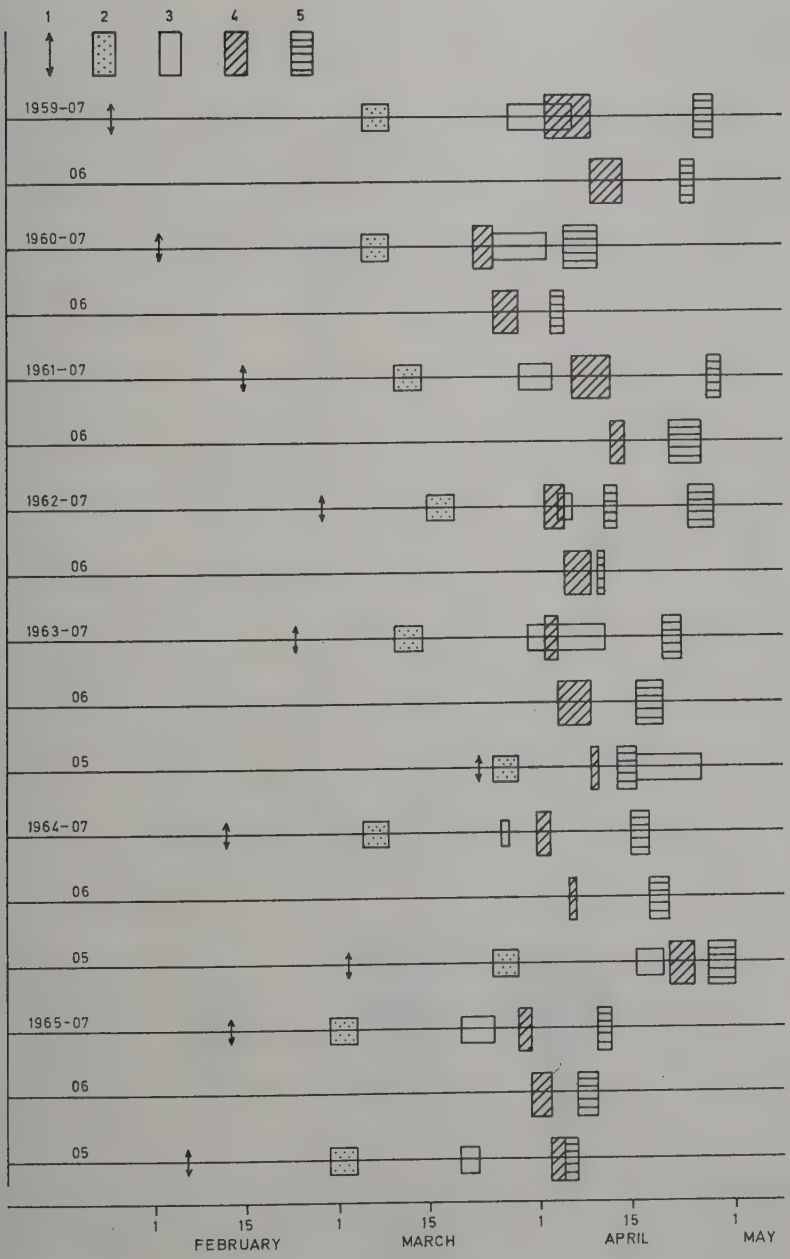


Fig. 6. Mean temperature at different spawning grounds within the main spawning regions in areas 07, 06 and 05, depth intervals from 50 to 200 m or to the bottom. The vertical bars show the quartile intervals.

ing the temperature range within the main spawning depths, were widest in 1959, 1960, 1963 and 1965 and this feature may have resulted in a variable incubation period (Fig. 7). The range was considerably more narrow in 1962 and 1964 and the time of main hatching, therefore, shorter. In the spawning regions off Halten–Sklinna and Lofoten (areas 06 and 05) the mean temperature followed the same trend as in area 07, but the quartile intervals in area 06 was not as wide as on the spawning grounds within area 07. Since the spawning occurred at different times off Møre (area 07) and Lofoten (area 05) in 1963 and 1964, the total hatching period was relatively long these years. In 1965 the spawning and hatching took place almost at the same time in the two spawning regions and the time of main hatching occurred relatively early, especially in area 05 (Fig. 7).

The commencement of the Norwegian winter herring fishery, coinciding in time with the arrival of spawners to the coast, the estimated time of the main spawning and hatching and the first and second periods of larval sampling are also plotted on the time scale in Fig. 7. On the Møre coast (area 07) the time of arrival of the herring, the spawning and the subsequent hatching all occurred progressively later during the period 1959–1962, whereas the opposite trend was found from 1963 to 1965.

Fig. 7. Time of, (1) commencement of the Norwegian winter herring fishery, (2) main spawning, (3) main hatching, (4) and (5) first and second annual periods of larval sampling.


1
2
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FEBRUARY
MARCH
APRIL
MAY

THE LARVAE

LARVAL DISTRIBUTION AND ABUNDANCE IN RELATION TO SPAWNING CHARACTERISTICS AND WATER CURRENTS

Soon after hatching the major part of the larvae rise into the upper water layers (50–0 m). Observations made at drift stations off Sklinna and Eggum indicated a vertical migration of the larvae (Fig. 8). During the dark, larvae were most abundant in the upper 20 m and by day they concentrated at a depth between 20 and 40 m. However, a higher net avoidance during the day might to some extent account for the variation in vertical distribution within the upper 40 m. Nevertheless the majority of the larvae did occur within the upper 50 m and were scarce in the depth range from 50 to 70 m.

The larvae are transported northwards mainly in coastal water, i.e. water with salinity less than 35‰ (Helland-Hansen and Nansen 1909). This water moves as a coastal current from the Skagerak to the Barents Sea, whereas Atlantic water (with salinity above 35‰) moves northward farther offshore with the core just outside the edge of the continental shelf. The main bulk of coastal water seems to be deflected northward off Stad (Fig. 9), and outside Møre the current has its maximum northward velocity at the edge of the shelf, whereas over the Møre plateau the current is weaker and on some occasions vortex movements of the water masses occur (Helland-Hansen and Nansen 1909, Ljøen and Nakken 1969). The branch of the coastal water which follows the slope northwards from about N 63° 15′, E 5° 40′ is mixed with salter and warmer water masses and will relatively soon lose its original characteristics (Ljøen and Nakken 1969). The main bulk of coastal water flows to the east off Ona–Grip and follows the coast northwards from Grip (Fig. 9).

The velocity of the coastal current varies greatly (Helland-Hansen and Nansen 1909, Eggvin 1940, Ljøen 1962). The subsurface drogue

Table 11. Subsurface drogue measurements in larval patches during the surveys in 1963–1965 and 1967.

Date		Drift station no.	Position	Duration of experiment in hours	Drifting velocity parallel to the coast in knots
1963	20–21.4	1	N 63° 44′, E 07° 52′	24	0.75
1964	18–19.4	2	N 65° 26′, E 10° 45′	24	1.08
	30.4	3	N 66° 33′, E 12° 02′	12	0.36
	28–29.4	4	N 68° 20′, E 13° 14′	24	0.29
1965	9–10.4	5	N 64° 20′, E 09° 32′	24	1.00
1967	3– 9.4	6	N 63° 06′, E 05° 51′	138	0.10 clockwise drift

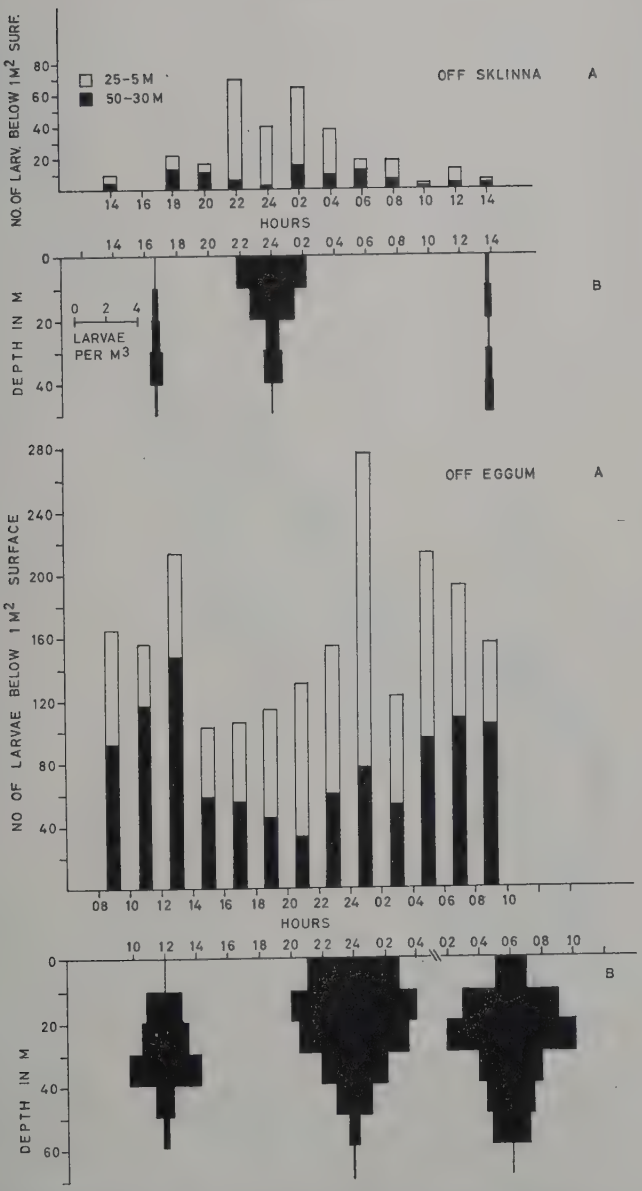

Fig. 8. (A) quantity of larvae caught in oblique hauls with CBPS during the survey in 1964 at drift stations 2 and 4 (off Sklinna and Eggum) during a 24-hour sampling period and (B) vertical distribution of larvae at the same stations.

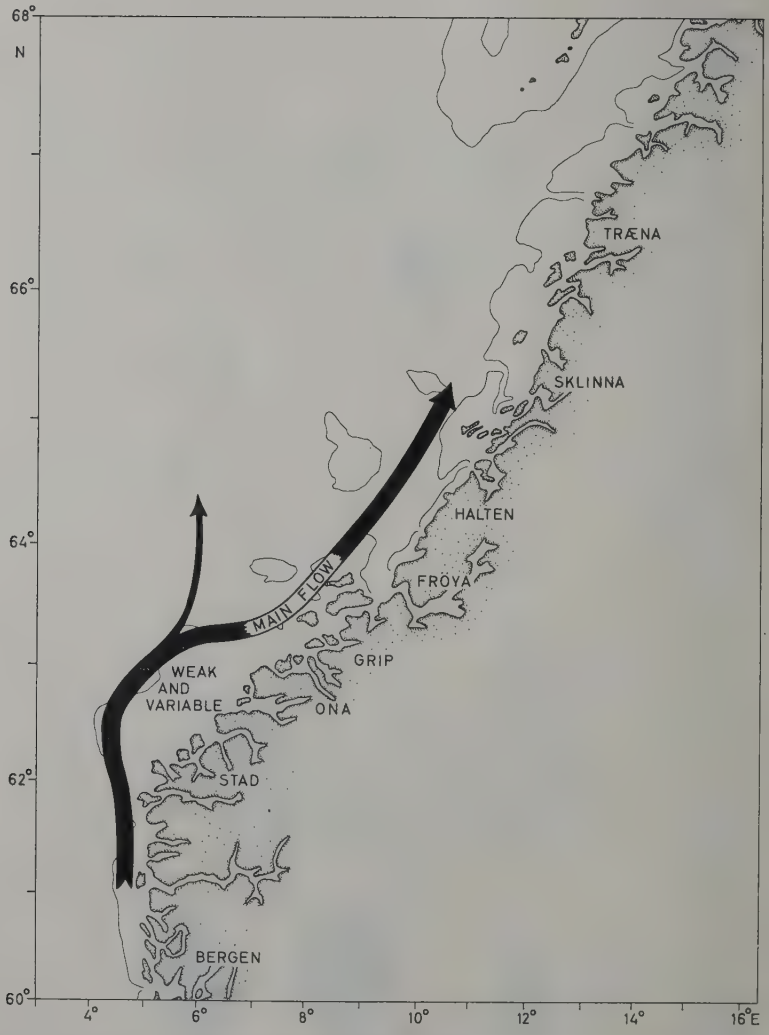

Fig. 9. Main flow of coastal water off Møre and Trøndelag (reconstructed from Ljøen and Nakken 1969).

measurements carried out at different places along the coast (Table 11) showed relatively high velocities off Frøya and Sklinna (stations 1, 2 and 5) and lower velocities farther north off Træna and Eggum (stations 3 and

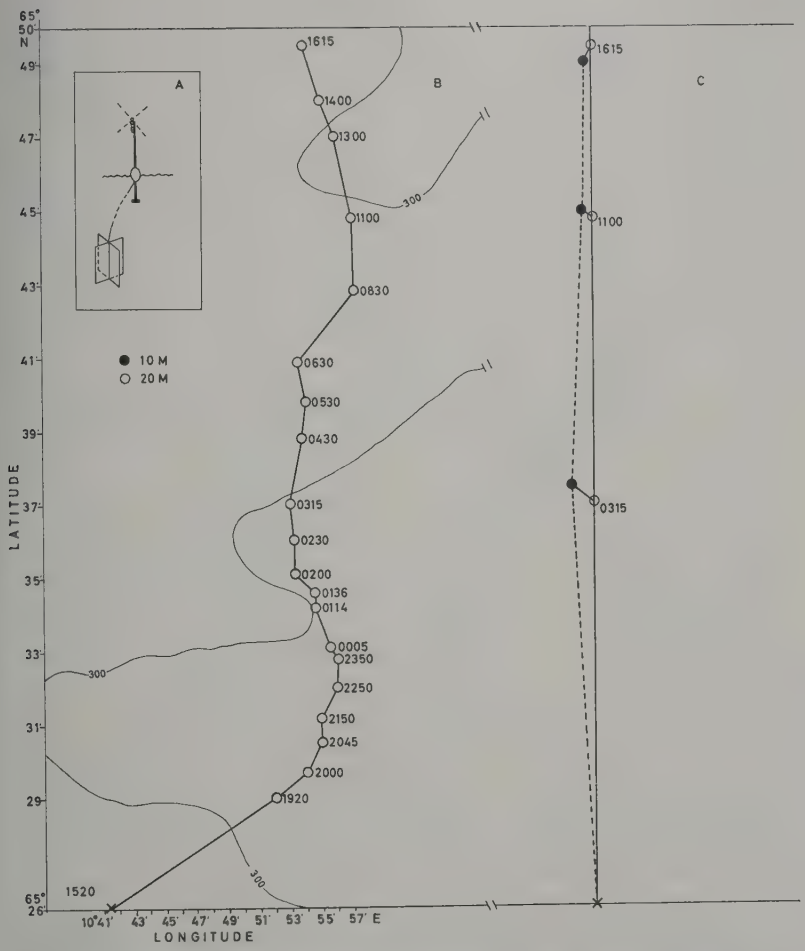

Fig. 10. (A) subsurface drogue, not drawn to scale, (B) drift path of a drogue at 20 m depth off Sklinna in 1964, from 18 April at 1520 hours to 19 April at 1615 hours (local time) and (C) positions of the drogue at 20 m depth compared with positions of drogue at 10 m depth.

4). On the shelf off Ona (station 6) a vortex movement took place during an experiment in 1967 (Dragesund and Nakken 1968). Thus the larval distribution and drift will vary depending on the location of spawning.

No important difference in the direction and velocity of the current was found between 10 and 20 m during the 1964 experiments (Fig. 10), and none was found between 10 and 40 m in an experiment carried out in 1965 (Dragesund and Hognestad 1966).

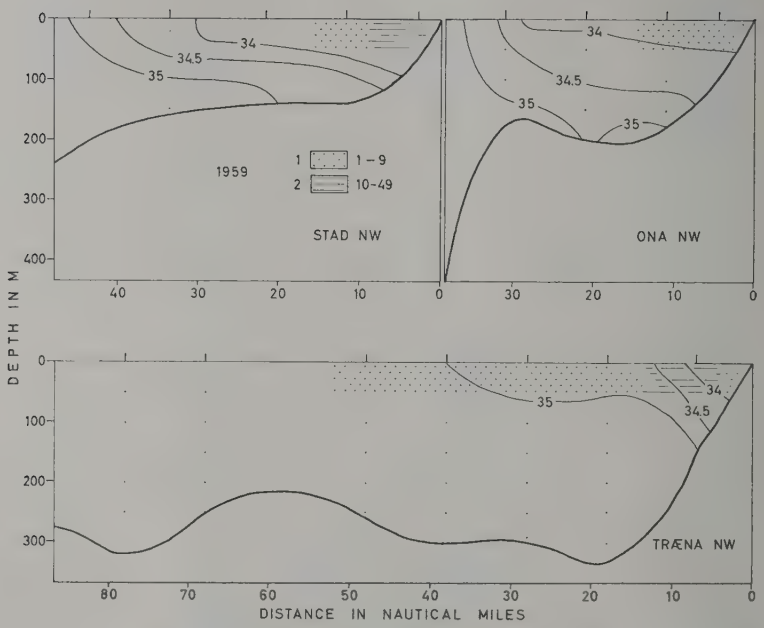

Fig. 11. Distribution of salinity (‰) in three vertical sections seaward from Stad, Ona and Træna, (1) and (2) number of larvae below 1 m² surface.

The seaward extent of larval distribution in 1959 in relation to the salinity distribution is shown in Fig. 11. All larvae in the two southernmost sections (off Stad and Ona) were found in coastal water, whereas farther north (off Træna) they were more dispersed and found also in Atlantic water. However, the most dense concentrations were observed in the core of coastal water where the main transport of larvae took place. The 35‰ isohaline at 0 m in relation to the larval distribution on the shelf between Stad and Lofoten is shown in Fig. 12.

Figs. 12–18 show the larval distribution in 1959–1965 during successive periods. The first survey in 1960 is not included as it was carried out prior to the time of main hatching (Fig. 7). In 1964 the first survey was omitted because sampling was made only at a few stations. The second survey of that year covered a relatively late period in relation to hatching in areas 07 and 06, but about the same period as in other years in area 05.

During the first annual survey period (Figs. 12–18A) the main larval concentrations from the spawning grounds in areas 07 and 06 were found between Stad and Sklinna, extending to the southernmost part of area

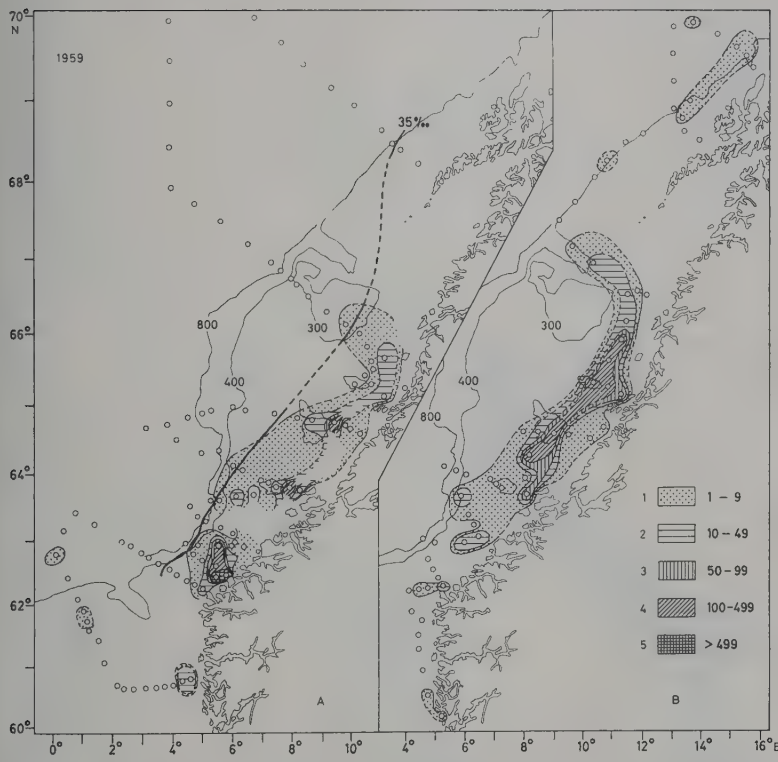

Fig. 12. Distribution of herring larvae in 1959, (A) all length groups (caught with Nansen net), 2–13 April, and the 35‰ isohaline at 0 m, (B) larvae ≥12 mm (caught with CBPS), 20–28 April. (1) to (5) number of larvae below 1 m² surface. Stations are plotted as circles.

07 in 1959–1961. In 1959, 1961, 1963 and 1964 the distribution in areas 07 and 06 was somewhat more wide than in 1962 and 1965. The distribution pattern was characterized by high larval concentrations near the coast, decreasing seaward and almost no larvae were found outside the edge of the shelf. In the years 1962–1965 larvae were scarce south of Ona, a result of the restricted spawning on the southern grounds.

In 1964 and 1965 the distribution was characterized by two main centres, one off the Møre–Trøndelag coast and the other off the coast between Træna and Eggum. In 1964 larvae from the spawning grounds off Møre (area 07) and Trøndelag (area 06) had already mixed with those from the Lofoten spawning grounds (area 05) when the survey was carried out, whereas in 1965 the larvae from the spawning off Møre–

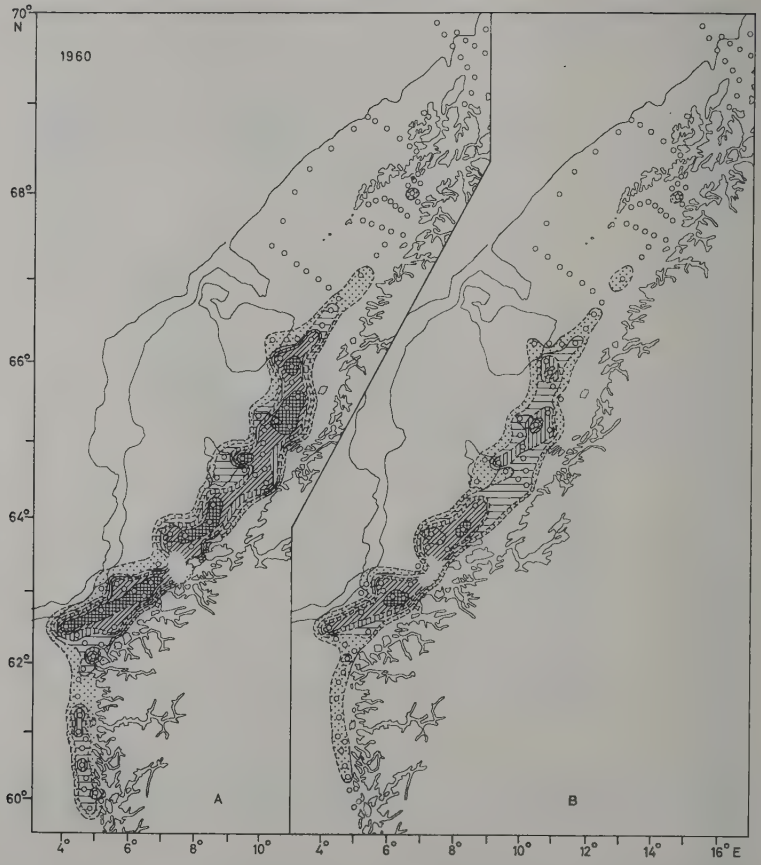

Fig. 13. Distribution of herring larvae 31 March–9 April 1960, (A) all length groups and (B) ≥12 mm. Legend as in Fig. 12.

Trøndelag were separated from those hatched at Lofoten. During April of 1964 and 1965 the major part of the larval population was located farther north than at the same time in earlier years (1959–1961), mainly because of the spawning at Lofoten.

In general the abundance of larvae was high during or immediately after the time of the main hatching, especially in 1960 (Fig. 19A). In 1962 and 1965 high catches were restricted to a limited region off Frøya, whereas in 1963 and 1964 relatively low catches were obtained at all sections (1959 is omitted due to lack of data with CBPS). In 1967 evidence

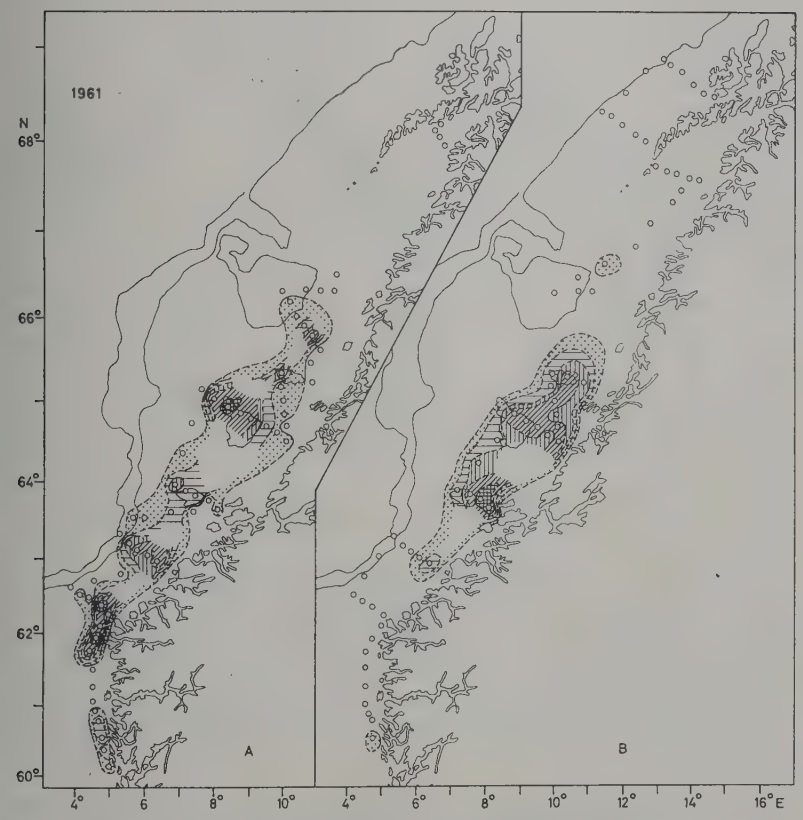

Fig. 14. Distribution of herring larvae in 1961, (A) all length groups, 6–19 April and (B) ≥12 mm, 20–29 April. Legend as in Fig. 12.

of a mass mortality of larvae off Møre soon after hatching (i.e. during the growth period between 10 and 12 mm of length) was found by Dragesund and Nakken (1968). When comparing the distribution and abundance of larvae in relation to subsequent year-class strength, therefore, those having passed the yolk sac stage (i.e. larvae ≥12 mm) should be considered separately.

In Figs. 12–18B the distribution of these larvae are shown during the second annual survey period. In 1961, 1962 and 1965 the post yolk sac larvae were concentrated off Frøya and were considerably less abundant south and north of this region. In 1961 larvae also were numerous off Halten. In 1959, 1960, 1963 and 1964 the larvae were more widely distributed. Because of the variable sampling time in relation to hatching, it

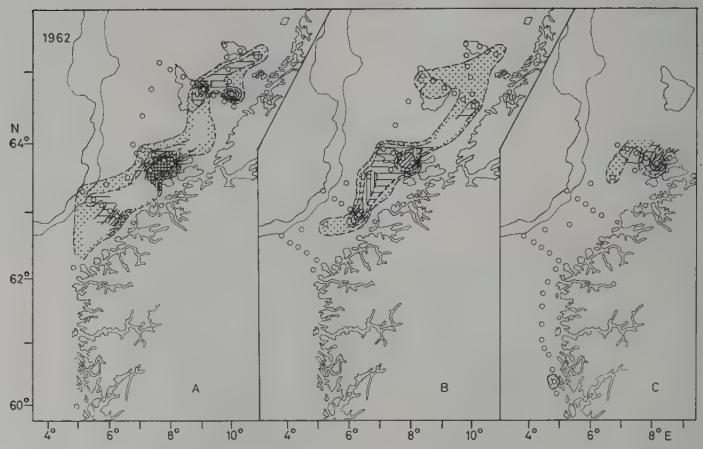

Fig. 15. Distribution of herring larvae in 1962, (A) all length groups, 2–9 April, (B) ≥12 mm, 6–13 April and (C) ≥12 mm, 24–28 April. Legend as in Fig. 12.

is difficult to make a quantitative comparison of the abundance estimates between years. Table 12 shows the percentage of larvae ≥12 mm and of larvae ≥15 mm during the second period of sampling. In 1959 96.3% of the larvae were ≥12 mm, whereas the corresponding figures for the following years were considerably lower, particularly in 1960. Larvae hatched off Lofoten were mainly below 12 mm in length at the time of sampling.

Table 12. Percentage of larvae ≥12 mm and ≥15 mm during the second annual sampling period for each of the years 1959–1965.

Date		Area	No. of stations	Total no. of larvae below 1 m² surface	≥12 mm	≥15 mm
1959	23–28.4	07 and 06	30	1435	96.3	53.0
	20–23.4	05	8	31	87.1	45.2
1960	2– 8.4	07 and 06	59	26445	21.9	0.0
	28.3– 2.4	05	2	9	0.0	0.0
1961	21–29.4	07 and 06	22	4824	84.1	13.6
1962	24–27.4	07 and 06	8	1047	32.9	2.7
1963	16–23.4	07 and 06	38	1809	66.1	2.5
	13–16.4	05	3	18	16.7	16.7
1964	13–20.4	07 and 06	34	1224	59.2	30.4
	20–30.4	05	51	3375	29.4	7.1
1965	7–12.4	07 and 06	27	2127	57.3	5.6
	4– 7.4	05	15	443	24.4	0.0

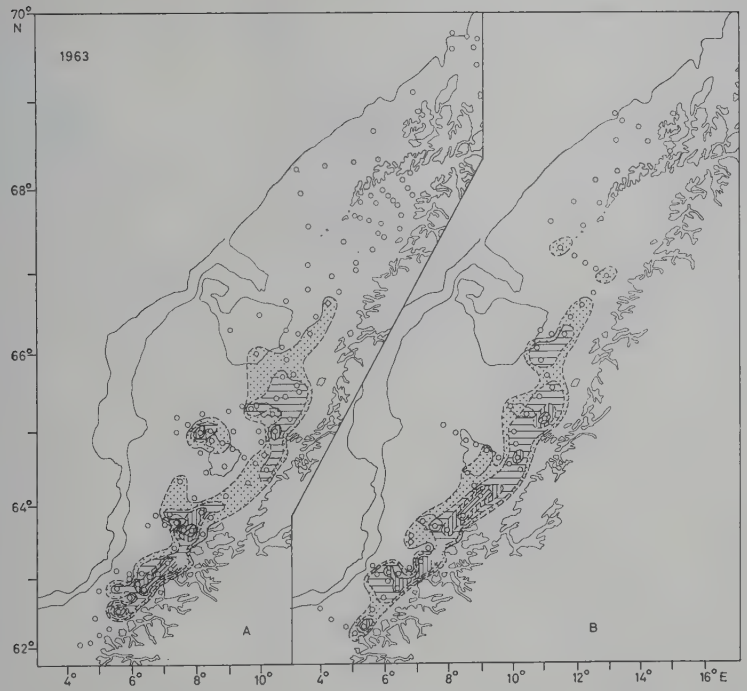

Fig. 16. Distribution of herring larvae in 1963, (A) all length groups, 2–10 April and (B) ≥12 mm, 13–23 April. Legend as in Fig. 12.

The number of larvae ≥12 mm and ≥15 mm per station at the sections off Stad, Ona, Frøya, Halten, Sklinna and Træna is illustrated in Fig. 19B (1960 is omitted). Less variable values were found at the different sections for post yolk sac larvae ≥12 mm in 1959, 1963 and 1964 than in 1962 and 1965. In 1961 a marked displacement northward had taken place between the two sampling periods, and the larvae were evidently more concentrated during the second than during the first period of sampling. The abundance off Frøya and Halten in 1961 was markedly higher than in the other years. The number of larvae ≥15 mm was low except for 1959 and 1961. More than 50% of the larvae caught in 1959 were ≥15 mm. This may have resulted in an underestimate of the abundance of the 1959 larvae compared with other years as the catching efficiency of CBPS is lower for larger than smaller larvae. Mortality from hatching up to the sampling stage adds also to this underestimate.

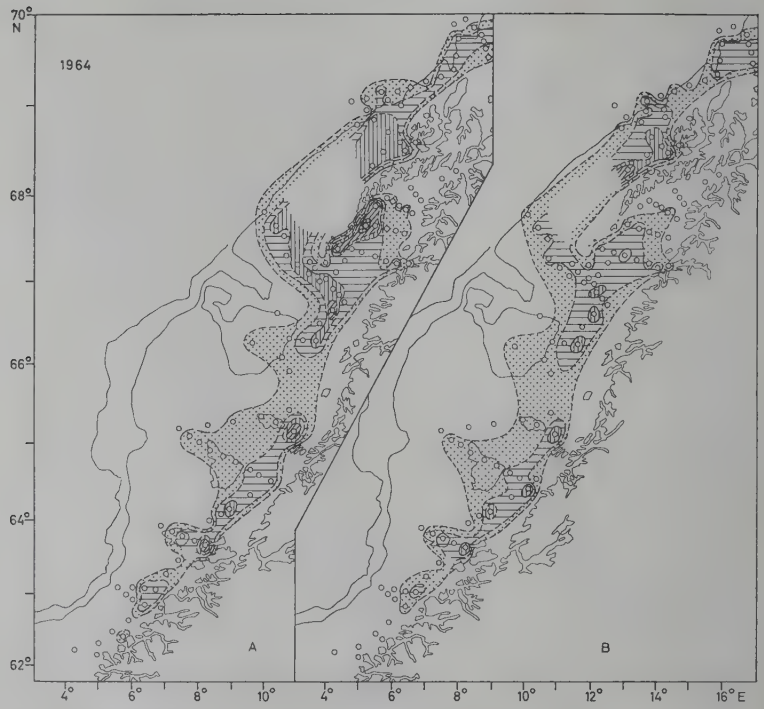

Fig. 17. Distribution of herring larvae 13–18 April 1964, (A) all length groups and (B) $\geq$12 mm. Legend as in Fig. 12.

The following characteristic features of the distribution and abundance of the larvae can be listed:

1) the abundance was relatively high during the post yolk sac stage in 1959;

2) the highest abundance just after hatching was found in 1960, and the exceptionally high figures found at all sections that year indicated a high hatching success over a wide spawning area;

3) the 1961 larvae were also numerous after hatching and throughout the post yolk sac stage, though more marked concentrated during the second than during the first period of sampling;

4) the 1962 and 1965 larvae were more concentrated and had a more patchy distribution than in other years;

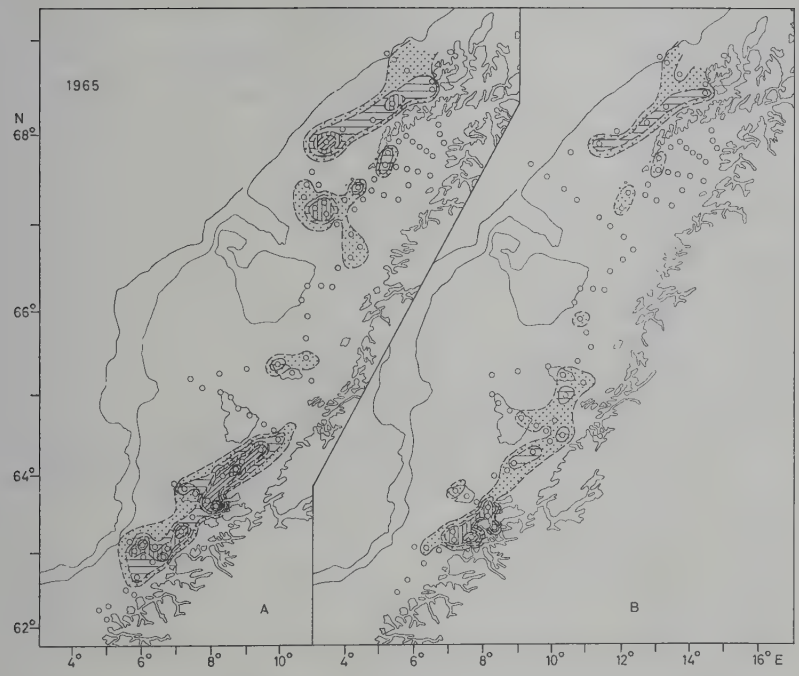

Fig. 18. Distribution of herring larvae in 1965, (A) all length groups, 29 March–6 April and (B) ≥12 mm, 4–12 April. Legend as in Fig. 12.

5) the distribution in 1963 and 1964 was widespread, particularly during the second period of sampling, but the abundance at the different sections were low;

6) the abundance estimates at the different sections between Stad and Træna suggest that the variation in the size of the spawning stock was reflected in the larval abundance figures obtained in the period just after hatching.

As indicated by the distribution charts (Figs. 12–18) a northward displacement of the larval concentrations in the southern part of the survey area was observed in most of the years. In the northern part of the area time intervals between surveys were too short to allow any marked northward drift to be recorded. However, in 1959 a displacement northward off Træna was traced. To illustrate the drift from a known spawning site near Grip, the larval distributions during two successive periods of the survey in 1968 are shown (Fig. 20). The spawning site was located on

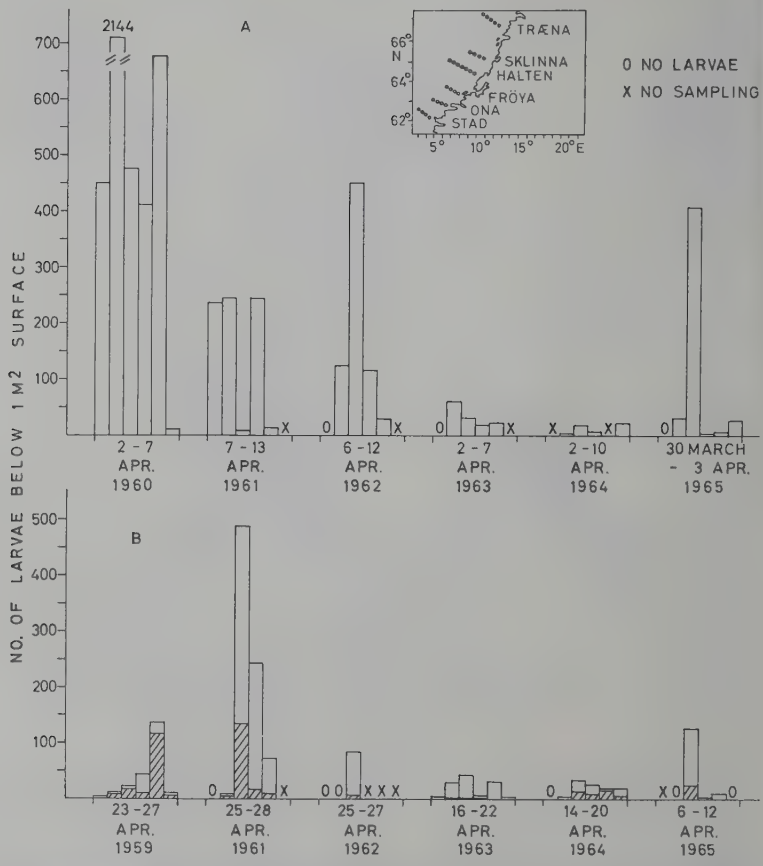

Fig. 19. Number of larvae below 1 m² of surface per station at six sections, from left to right: Stad, Ona, Frøya, Halten, Sklinna and Træna, (A) larvae of all length groups, (B) of larvae ≥12 mm and ≥15 mm (diagonal shading).

23 March when eggs were collected with dredge. Adult herring were recorded near the bottom some days earlier at the same locality. The eggs were examined and fertilization was estimated to have taken place from 5 to 10 March. Further inspections were carried out from 25 to 31 March, and the larvae were now nearly at the hatching stage. A detailed sampling programme was started, and during the following few days larvae were numerous just north of the spawning site. Assuming that the majority of the larvae were derived from this spawning site, the drift was

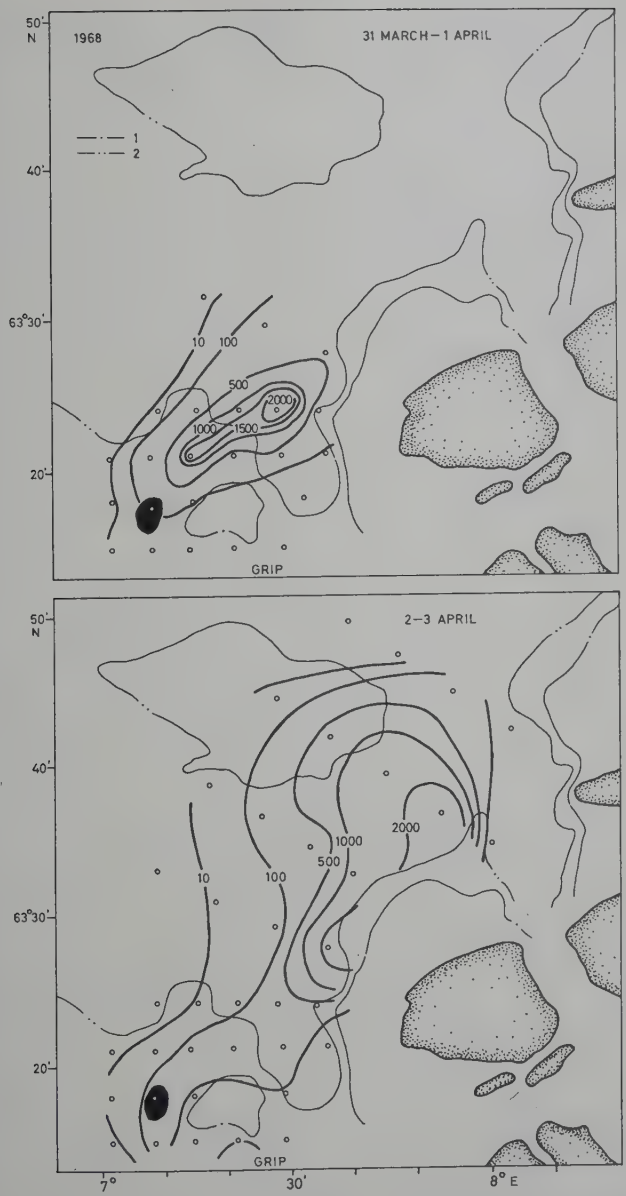

Fig. 20. Larval dispersion from a spawning site (black) off Grip. Isolines indicate the number of larvae below 1 m² of surface, (1) and (2) are the 100 and 200 m contour lines, respectively.

estimated to 0.67 knots by measuring the distance between the centres of concentrations in two successive sampling periods. The estimated drifting velocity was slightly lower than indicated by the subsurface drogue measurements farther north off Frøya and Sklinna in 1963–1965 (Table 11).

Since the larvae are mainly found in the upper 50 m, it may be assumed that the force and direction of the wind play an important role in determining the distribution pattern of larvae. Although the coastal current is directed northward, the surface water may be turned in various directions by the wind force. In periods with southerly winds the larvae will be transported northwards relatively quickly, whereas the drift will be hampered when winds from north prevails as the wind produces not only a pure wind current to the right of the wind direction, but also a relative current that runs parallel to the coast (Ekman 1923, Sverdrup, Johnson and Fleming 1946). Therefore, wind data from the meteorological stations Ona, Nordøyane and Skomvær have been analysed (Fig. 21).

The wind distribution in 1961 presumably resulted in a rather strong northward flow of water in the southern area but a weak northward flow in the northern area. In 1962 the same trend was found, although the wind vectors were smaller. In these years the wind distribution thus may have hampered the northward drift of the larvae from the spawning region in area 06, and may also partly have accounted for the high concentrations of larvae found between Frøya and Halten. For 1959, 1960, 1963 and 1964 the wind vectors indicate a prevailing strong northward flow of water resulting in more widespread north–south distribution of larvae.

The larval drift also may be studied in relation to the distribution of recovered drift bottles released in larval patches at various places during the surveys in 1961 and 1963–1965 (Fig. 22). All the bottles recovered in 1961 were found within thirty days after release in the coastal belt, and the high frequency of returns indicates that they were transported northwards close to shore. The 1963 recoveries showed a quite different distribution. None of the bottles released was recaptured within thirty days, and all the returns are from areas farther north (areas 05, 04 and 03). This distribution indicates that the bottles drifted northwards at some distance from the coast during the first period after release. Bottles released in 1964 and 1965 in area 07 were frequently recovered in areas 07 and 06, indicating a drift nearer to the coast in those years. Bottles recovered within sixty days in 1964 were distributed somewhat farther north than in 1965, indicating a faster drift in 1964. The drift of bottles along the coast from Møre to Finnmark was clearly demonstrated, and it is likely that larvae hatched off Møre are transported to this area.

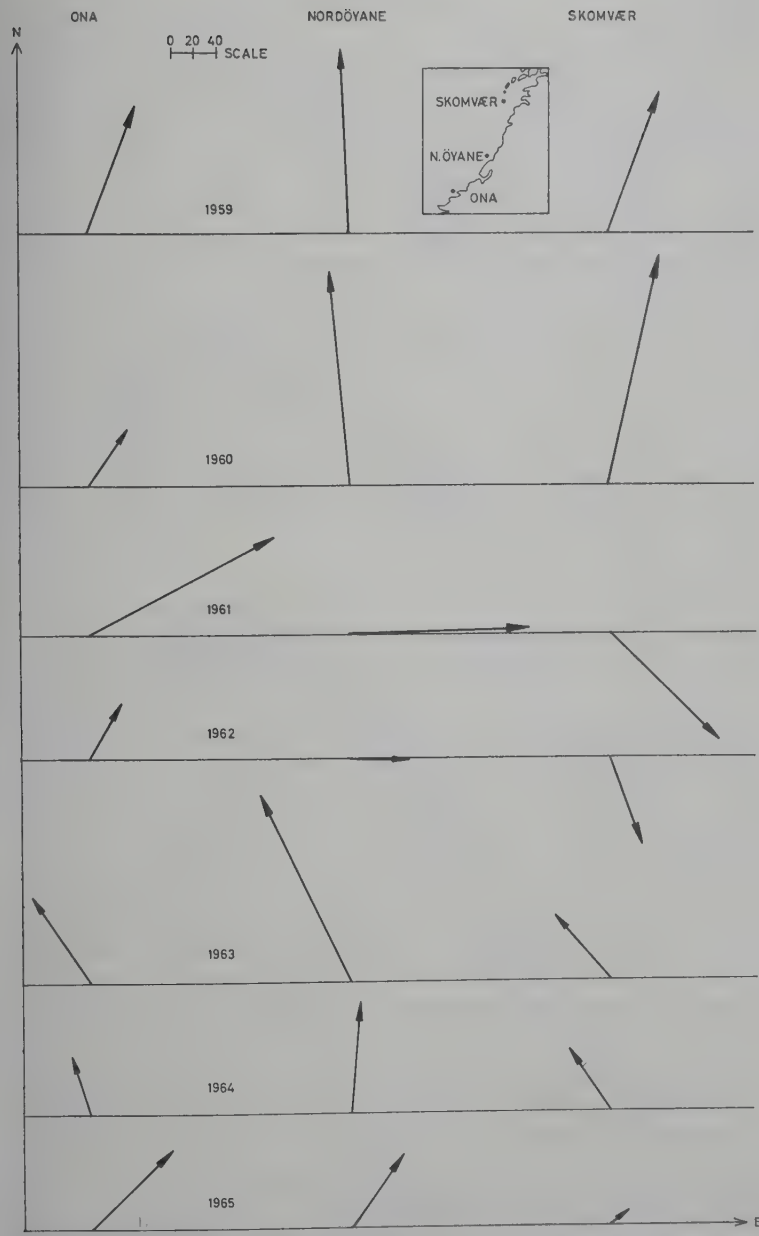

Fig. 21. Average resultant wind vectors for the period March–April in 1959–1965.

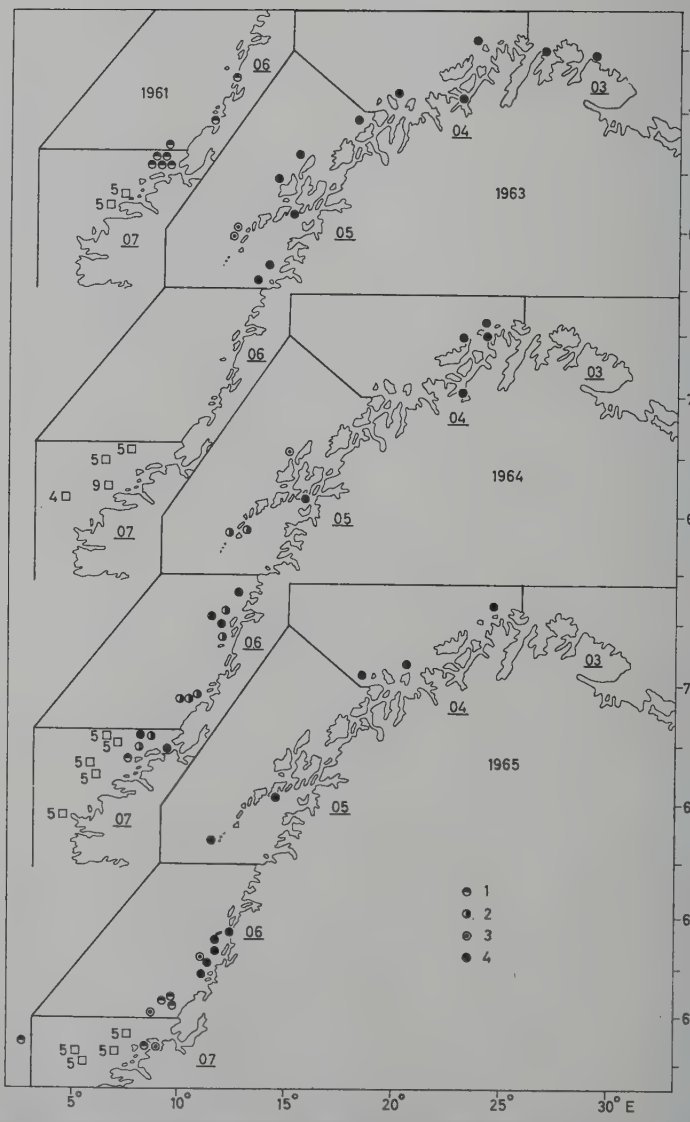

Fig. 22. Drift bottle experiments in 1961 and in 1963–1965. Open squares denote positions of releases and circles distribution of recoveries, (1) within 30 days, (2) between 31 and 60 days, (3) between 61 and 90 days and (4) more than 90 days after release. The number of drift bottles released at each position is listed in the figure.

The general drift pattern of larvae can be summarized as follows:

1) an extensive northward drift of larvae takes place from all the spawning grounds along the coast;
2) larvae hatched south of Stad will probably be transported northward near the coast, but a more offshore distribution is possible when they pass the region off Møre;
3) larvae drifting northward along the coast may follow a vortex movement over the southern part of the Møre plateau;
4) larvae being transported offshore will most likely be deflected towards the coast again off Grip–Frøya where the northward flow is relatively rapid before it slows down again off the coast between Træna and Lofoten;
5) during the northward drift part of the total larval population will accumulate at the entrance of the fjords along the Norwegian coast, and this part is probably greatest when the spawning takes place in the southernmost region (within area 08).

LARVAL LENGTH IN RELATION TO TIME OF SPAWNING

The length distribution of larvae in different regions between Bergen and Andenes is shown in Figs. 23 and 24. During the first period of sampling in 1959–1961 larger modal lengths were found between Stad–Ona and Grip–Frøya than south and north of these regions. It is assumed, therefore, that spawning started in the central part of the main spawning district (i.e. between Stad and Ona), and that the onset of spawning occurred slightly later to the south and north of this area. In 1962–1964 the largest modal lengths were found off Grip–Frøya, indicating that spawning started first between Ona and Grip. However, in 1962 only small differences in lengths were found in relation to both region and time. The late onset and the restricted duration of spawning that year presumably led to a mass spawning over a relatively short period resulting in smaller variations in lengths. Similarly, no marked trends were found in the length distributions of larvae between Stad and Halten in 1965. This suggests simultaneously hatching on all spawning grounds.

Table 13 lists the coefficients of variation (v) for the different length distributions

$$v = \frac{s}{\bar{l}} 100$$

where s is the standard deviation and $\bar{l}$ the mean length.

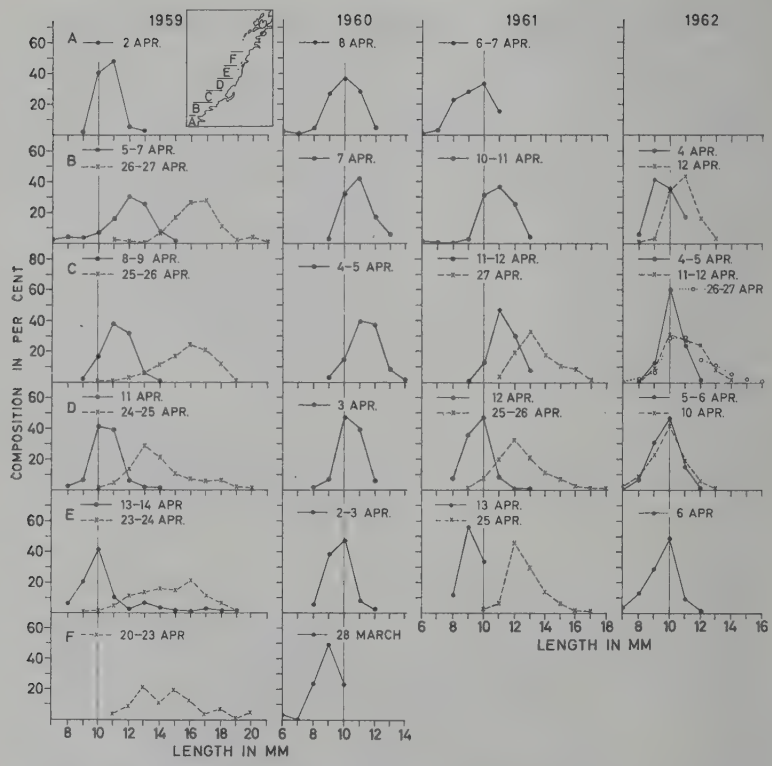

Fig. 23. Length distribution of larvae caught with CBPS in 1959–1962, (A) Bergen-Kinn, (B) Stad-Ona, (C) Grip-Frøya, (D) Halten, (E) Sklinna and (F) Træna. Data on larval lengths from CBPS and Nansen net are pooled for the second part of the 1959 survey (20–27 April). Prior to this period the larvae were caught with Nansen net.

The coefficients were relatively high in 1959, reflecting the long duration and low rate of spawning (Table 10). Although the spawning seasons were long, the coefficients of variation for 1960 and 1961 were lower than for 1959, suggesting that the main hatching was concentrated over a shorter period these years. This is also supported by the relatively high spawning rate and the high numbers of larvae per station in 1960 and 1961 (Fig. 19).

In 1964 the length distributions were bimodal in most of the regions during the second period of sampling, probably because of the difference in spawning time between the spawning regions off Møre–Trøndelag and off Lofoten and also within the Møre–Trøndelag spawning regions. The

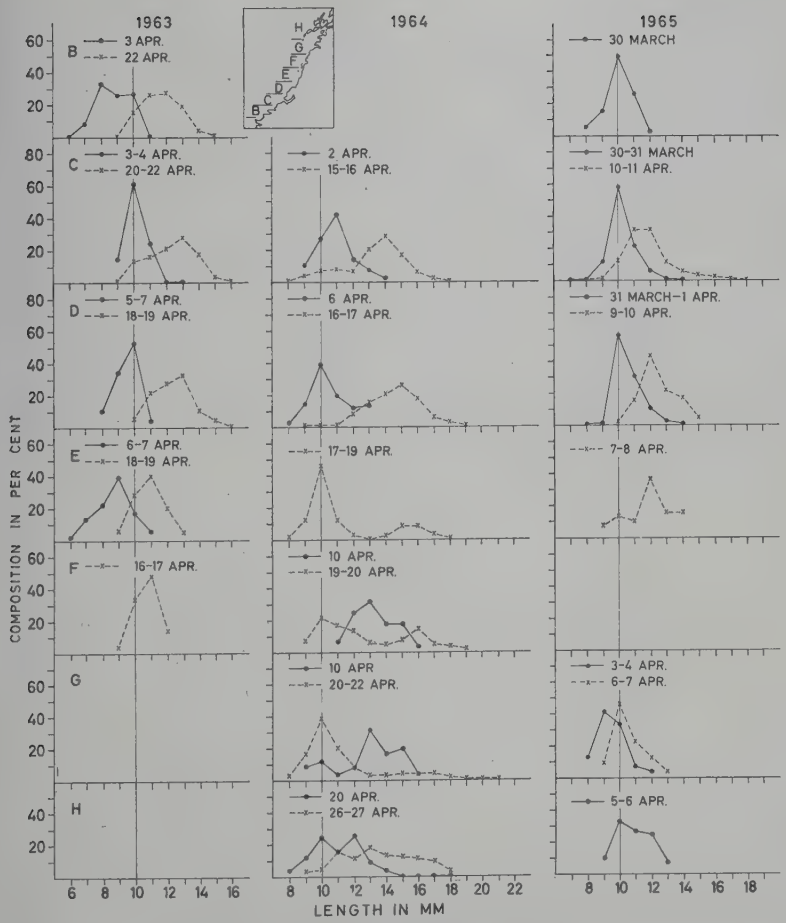

Fig. 24. Length distribution of larvae caught with CBPS in 1963–1965, (B) Stad-Ona, (C) Grip-Frøya, (D) Halten, (E) Sklinna, (F) Træna, (G) Lofoten and (H) Eggum-Andenes.

age composition of the spawners may explain the differences in spawning time between and within the regions, the recruits spawning later in the season than repeat spawners. The largest larvae found in area 06 may have been produced by old fish which spawned relatively early in the season, whereas the smaller larvae probably originated from recruits which spawned slightly later. The larger larvae caught between Lofoten and Andenes were most likely transported from spawning grounds south of this region.

Table 13. Coefficients of variation (v) for larvae caught in different regions between Bergen Andenes during the larval surveys in 1959–1965.

Region	1959			1960			1961		
	Date	No.	v	Date	No.	v	Date	No.	
Bergen-Kinn	2.4	39	7.1	8.4	122	9.8	6–7.4	129	1
	28.4	8	14.3	—	—	—	—	—	
Stad-Ona	5–7.4	443	14.1	23.3	114	13.1	10–11.4	245	
	26–27.4	101	10.7	7.4	499	7.8	28.4	22	
Grip-Frøya	8–9.4	141	8.6	23.3	294	8.8	11–12.4	383	
	25–26.4	139	10.8	4–5.4	400	7.5	27.4	630	1
Halten	11.4	120	9.7	24.3	38	—	12.4	254	
	24–25.4	133	14.4	3.4	148	7.0	25–26.4	1074	1
Sklinna	13–14.4	65	22.4	25.3	123	7.7	13.4	142	
	23–24.4	450	14.0	2–3.4	400	6.9	25.4	344	
Træna	20–23.4	65	14.8	28.3	55	9.1	—	—	

	1962			1963		
Stad-Ona	4.4	53	8.8	3.4	175	11.4
	12.4	378	8.2	8.4	29	7.3
	—	—	—	22.4	161	10.3
Grip-Frøya	4–5.4	1339	6.5	3–4.4	271	6.1
	11–12.4	1129	11.1	7–8.4	266	7.6
	26–27.4	674	13.4	20–22.4	341	11.8
Halten	5–6.4	509	9.1	5–7.4	50	7.7
	10.4	480	10.9	18–19.4	190	9.8
Sklinna	6.4	277	9.7	6–7.4	139	11.3
	—	—	—	18–19.4	139	8.2
Træna	—	—	—	16–17.4	56	6.6

	1964			1965		
Stad-Ona	—	—	—	30.3	38	8.7
	—	—	—	—	—	—
	—	—	—	—	—	—
Grip-Frøya	2.4	46	10.1	30–31.3	1419	7.7
	15–16.4	110	14.6	10–11.4	756	12.1
Halten	6.4	42	12.3	31.3–1.4	835	7.6
	16–17.4	107	6.3	9–10.4	56	9.0
Sklinna	17–19.4	144	22.5	2.4	14	3.0
	2.5	45	27.5	7–8.4	38	12.4
Træna	10.4	29	9.9	—	—	—
	19–20.4	185	21.2	—	—	—
Lofoten	10.4	37	15.2	3–4.4	132	10.2
	20–22.4	503	21.1	6–7.4	103	9.6
	29–30.4	104	23.0	—	—	—
Eggum-Andenes	20.4	84	18.0	5–6.4	110	10.2
	26–27.4	78	16.4	—	—	—
	27–29.4	290	13.2	—	—	—

Also the mixture of relatively young recruit spawners and old repeat spawners (off Møre and Trøndelag) may have contributed to the expanded bimodal length distribution of larvae. According to Blaxter and Hempel (1963) and Hempel and Blaxter (1967) young recruit spawners produce slightly smaller eggs and hence smaller larvae. The difference in egg weight between the youngest recruit spawners and the next age group in Norwegian herring was about 10–14%, so the difference in egg size and spawning date worked in the same direction and contributed to the bimodal length distribution of larvae.

No such bimodality in the length distribution was found in 1965 when both young recruits and old repeat spawners were present on the southern spawning grounds off Møre. However, the old fish made up only 15–20% of the stock in this region. In 1965 both the duration and the time of main spawning were nearly the same over the entire spawning area from Ona to Lofoten. This resulted in smaller length variations compared with 1964.

DISCUSSION

SPAWNING CHARACTERISTICS

The relationship between year-class strength and the following factors will be discussed:

1) age structure and size of the parent stock;
2) location of spawning;
3) duration and time of spawning.

The effect of the age structure of the parent stock on the year-class strength has been discussed by Marti (1959) and Bridger (1961). They suggested that older herring produce bigger eggs resulting in stronger larvae with better yolk reserves. Blaxter and Hempel (1963) found that the egg size and survival time on yolk reserves depend little on the age structure of the parent stock, although very young recruits produce slightly smaller eggs and larvae. Thus, in years when the stock consists mainly of very young spawners, the viability of the progeny may be reduced. During the 1950s young recruits were relatively abundant in 1954 (Østvedt 1963). In the period 1959–1965 the influx of young recruit spawners was highest in 1964 and 1965, but also in 1963 recruits of the 1959 year-class appeared on the spawning grounds in significant numbers. The 1963 and 1964 year-classes were of average strength, whereas those of 1954 and 1965 were very poor (Fig. 25). From 1955 to 1962 repeat spawners and relatively old recruits dominated in the stock, and in most

of these years poor year-classes were produced. Accordingly no apparent relationship can be established between the age structure of the parent stock and subsequent year-class strength.

In Fig. 25A the absolute size of the parent stocks for the period 1947–1962 is plotted against subsequent year-class strengths at six years of age. The absolute size of the spawning stocks during the period 1947–1952 has been derived from data given by Østvedt (1963). The abundance indices showed that stock size remained at about the same level during this period, and was somewhat lower than that which occurred in the mid-1950s. The average abundance figure for the stock size during the period 1947–1952 was about 83% of the average figure for the years 1954–1956.

Estimates of year-class strength for adults are complicated by the wide range of ages over which individuals of a given year-class attain sexual maturity. However, knowing the size of the spawning stock, an estimate of year-class strength can be obtained by calculating the abundance of the year-class at an age when most of the year-class has entered the adult stock. According to Østvedt (1958) the mean age at first spawning for herring of northern growth type (slowly growing herring) varies between 5.1 and 7.5 years, and for herring of southern growth type (rapidly growing herring) between 4.1 and 4.5 years. The strength of a year-class as adults, therefore, has been estimated at an age of six years (Fig. 25A).

During the period 1947–1962, two exceptionally rich year-classes were spawned, those of 1950 and 1959. The 1959 year-class was spawned when the adult stock was about half the size of that in 1950. During the period 1947–1956 the spawning stock was two to three times larger than in 1959, without producing any rich year-classes. In 1957 and 1958 the stock was also more abundant than in 1959, and again very poor year-classes occurred. The survival of the herring spawned in 1959 must have been relatively high since a rich year-class was spawned by a much smaller spawning stock than the stock which was present during the previous eight years. Similarly the survival was relatively high for herring spawned in 1960, although markedly lower than for those spawned in 1959. The 1962 year-class was very poor, being of the same magnitude as the year-classes spawned during the 1954–1958 period. The 1963–1965 year-classes had not reached the adult stage in 1968 and cannot be compared with the previous year-classes in the adult stock. Investigations carried out during the 0-group stage (Dragesund 1970) indicated that the 1963 and 1964 year-classes were slightly more abundant than that of 1961, whereas the 1965 year-class was very poor and probably less abundant than that of 1962 (Fig. 25B).

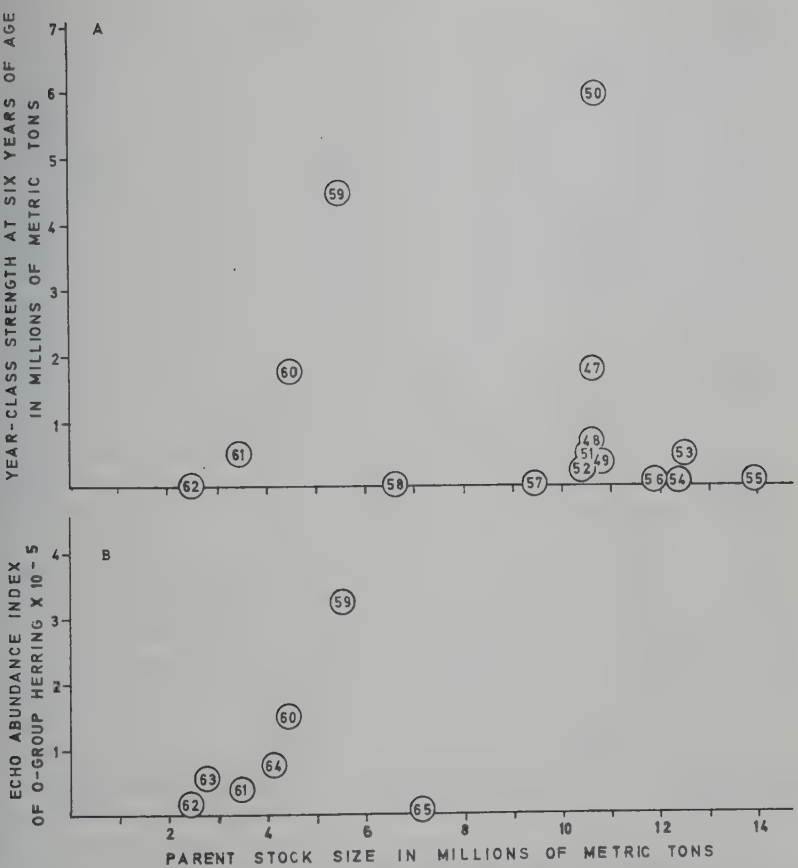

Fig. 25. Relationship between the parent stock size and the subsequent year-class strength, (A) at six years of age for the 1947–1962 year-classes and (B) at about six months of age for the 1959–1965 year-classes. The respective year-classes are indicated inside each circle.

The correlation diagram suggests that within the period considered, a relationship existed between the stock and the abundance of the resulting year-class when conditions for the progeny were favourable. However, in most of the years year-class strength was determined by other factors which completely ruled out the effect of the size of the parent stock. Thus, in at least twelve of the nineteen years during the period 1947–1965, the size of the parent stock has apparently not been the primary factor controlling subsequent year-class strength. In the years when numerous year-classes were produced as in 1950 and 1959 other factors (as for

instance a more widespread distribution of the spawning grounds and a longer duration of spawning) may have given rise to favourable conditions for the progeny.

In the years 1948–1959 the main spawning took place gradually farther north (Devold 1963) and in 1959–1965 the most important spawning centre was concentrated within area 07 between Stad and Grip. The main spawning grounds within area 06 were located off Halten–Sklinna, and no change in location could be recorded in this area during the period of investigation. In the 1950s spawning off Halten–Sklinna was observed by Wiborg (1954, 1956) and Yudanov (1962). The locations of spawning off Møre–Trøndelag given by Yudanov for the period 1959–1965 agree fairly well with the results of the present investigation. Spawning in the area 05 took place mainly during the period 1963–1965. Yudanov (1962, 1964, 1966) found insignificant spawning in the Lofoten region in 1959, 1961 and 1962, whereas in 1960 a major spawning was found on the banks between Lofoten and Andenes. Spawning in this region has also occurred in previous years as pointed out by Runnstrøm (1934), Awerinzew (1935), Rass (1939) and Marti (1956).

In the 1930s spawning was found at certain places along the entire coast from Lindesnes to Vesterålen (Runnstrøm 1934, 1941a), i.e. off the southwest coast between Lindesnes and Bergen, off the Møre coast and on the banks off Lofoten. The most important spawning region during this period, however, was located within area 08 off the southwestern coast of Norway. Thus, a general restriction of the spawning area has taken place during the 1950s and 1960s, especially in the southernmost spawning region (within area 08) at the same time as the main spawning centre moved farther north. The probability is that the spawning area is more extensive when the spawning stock is large than when the stock size is small. Also the age structure of the spawning stock may have an effect on the extension of the spawning area. However, the change and restriction in spawning area found in 1959–1962 could not only be attributed to the decrease in the size of the spawning stock but also to a real shift in the spawning migration.

Devold (1963) demonstrated that the stock arrived at the coast in area 07 increasingly farther north during the period 1950–1962. During the early 1950s a major part of the stock migrated southward along the coast for spawning, but this did not occur after 1959. The fact that herring shift from one spawning ground to another during their life span is also supported by tagging experiments (Dragesund 1961, 1962). Herring tagged on the spawning grounds between Bokn and Stolmen in 1957 and 1958, migrated to the spawning grounds off Møre–Trøndelag the following years. Moreover, the stock component spawning off Lofoten during

the period 1963–1966 did not appear on these spawning grounds the following two years, but mixed with the component migrating towards the spawning grounds off Møre–Trøndelag (Devold 1968, Jakobsson 1968). This change in location of maximum spawning may have resulted in a simultaneous change in the time of spawning.

To investigate the relationship between the duration of the main spawning period and subsequent year-class strength, the spawning rate has been plotted against year-class strength at six years (Fig. 26A) and at six months (Fig. 26B). The diagrams suggest that high spawning rates resulted in poor year-classes, whereas in years when the main spawning was prolonged stronger year-classes were produced. However, this did not fit in for all year-classes, e.g. those of 1951 and 1953–1955. Long spawning periods often result in prolonged hatching, and it is possible that a larger number of larvae can find suitable and abundant food when they are hatched over a long period than when hatching is restricted in time.

Within the period 1950–1965 the time of main spawning varied (Fig. 5), but no special trend in variation was found. However, in general the main spawning occurred later than it had previously in this century (Aasen 1962, Devold 1963). Between 1904 and 1920 the adult herring arrived at the coast already in October to December, and the main spawning, which took place within area 08, probably commenced earlier than at present time. During the period from 1929 to 1959 the spawning time changed markedly in the spawning region within area 08 (Fig. 27). From 1929 to 1932 the main spawning took place at the beginning of February, and from 1933 to 1939 it occurred in the second half of February. The main spawning time for the period 1929–1939 has been derived from data of Rasmussen (1940) by adding ten days to the onset of spawning given in his paper. During the 1950–1959 period the spawning in area 08 occurred during the first half of March. In area 07 (i.e. between Kinn and Grip) no marked change could be found, although the spawning in 1961–1963 took place somewhat later than in the previous years.

During the last three decades the main spawning time thus changed simultaneously with a progressively northward displacement of the main spawning centre. The change in location of maximum spawning and the variations described in spawning time may have resulted in variations in the environmental conditions for the larvae during the period just after hatching. The most striking change is the absence of spawning on the southernmost grounds, between Bokn and Stad, since 1959. In the 1930s and 1940s when the main spawning took place in this region, rich year-classes occurred more frequently (Marti and Fedorov 1963, Devold 1963). On the other hand, in the period 1904–1920 when spawning also

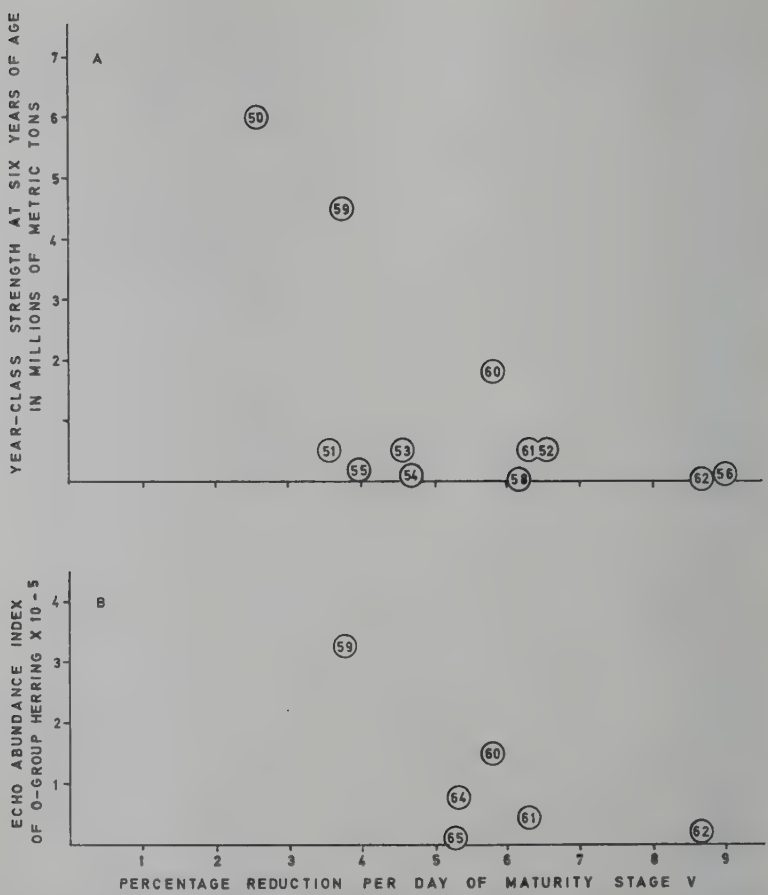

Fig. 26. Relationship between the spawning rate (percentage reduction per day of maturity stage V) within areas 08 and 07 during the spawning seasons in 1950–1965 and subsequent year-class strength, (A) at six years of age for the 1950–1962 year-classes and (B) at about six months of age for the 1959–1965 year-classes. The 1957 and 1963 year-classes are omitted due to insufficient data. The respective year-classes are indicated inside each circle.

took place in the same region, only two rich year-classes were spawned, those of 1904 and 1918. However, during this period the spawning most likely occurred somewhat earlier than in the 1930s (Runnstrøm 1934, Devold 1963), and this feature may have accounted for the long intervals between the appearance of rich year-classes.

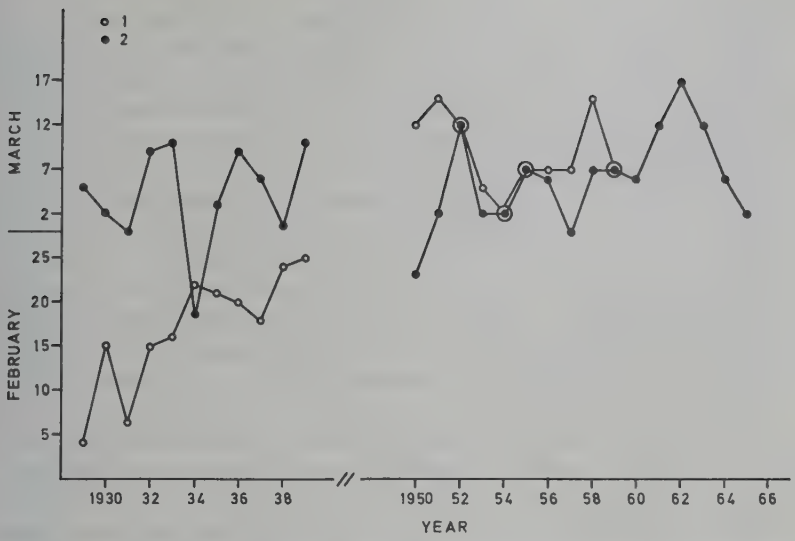

Fig. 27. Time of main spawning during the periods 1929–1939 and 1950–1965, (1) within area 08 and (2) within area 07.

ENVIRONMENTAL CONDITIONS DURING THE EGG STAGE AND EARLY LARVAL DEVELOPMENT

Considerations of environmental factors and their effects on developing eggs and larvae have mainly been concerned with the temperature and thickness of the egg layers. More recently, attention has also been drawn to other factors, as for instance predator effect, pollution and mechanical forces.

Postuma (1968) showed a relationship between the temperature on the spawning bed and year-class strength for Downs and Bank autumn spawning herring and suggested that optimum conditions existed at around 12°C. In the 1930s, when the main spawning of Norwegian herring took place in the southern spawning region (area 08), the most frequent bottom temperature during the spawning season was between 5 and 6°C (Runnstrøm 1941b). During the period 1959–1965, when maximum spawning took place farther north, the temperature varied between 5.5 and 7.5°C on the spawning grounds between Møre and Lofoten. The temperature on the main spawning grounds during the incubation period did not vary markedly from one year to another and cannot be associated with the year-class strength variations during the period 1959–1965.

Lea (1930) showed that thick egg layers on the Norwegian spawning grounds resulted in a high mortality since eggs in the deepest layers were

subjected to oxygen deficiency. Runnstrøm (1941b) did not find a distinct increase in mortality with increasing density of eggs, except in extremely thick egg layers (10,000 to 12,500 cm^3 per m^2 of sea bed), and the average mortality for the total egg material collected was 12.1%. In the Firth of Clyde, Parrish *et al.* (1959) showed that only very few dead and unfertilized eggs occurred in the samples, but the stage of development varied through the egg layer. Recent investigations in same area by Baxter (1968) showed average figures of 3–6% for dead eggs, and there was little indication of higher mortality in the lower layers. For North Sea herring mortality rates of 0–11% (average 4%) were found by Hempel and Hempel (1968). Dragesund and Nakken (unpublished) also observed few dead and unfertilized eggs on a spawning site near Grip in 1968. None of these results include mortality at the hatching stage, and mortality during the egg stage seems to be relatively low.

However, gadoid fish feeding on herring eggs have frequently been recorded on the spawning grounds both in the North Sea and along the Norwegian coast. Nothing is known about the frequency of stomach fillings per fish during the spawning season or of the number of fish feeding on herring spawn. The stomach of an adult haddock normally can contain at least the annual egg production of one herring per filling (Hempel and Hempel 1968, Dragesund and Nakken unpublished). Therefore, the predator effect may be of some importance.

A second phase of mortality occurs during the hatching period. Experiments carried out on Pacific herring (Galkina 1968, Taylor 1968) indicated that in dense concentrations of eggs the hatching success is rather low. The experiments by Taylor showed that the production of viable larvae per unit area often was lower when eggs were packed in eight than when only in four layers. It is not known if these results are applicable for larger stocks of herring reproducing in the open sea. However, Lea (1930) believed that conditions were more favourable for hatching when small quantities of eggs were distributed over a large area than when the spawning was concentrated in a limited region. The present material cannot be used for an analysis of egg concentration in relation to year-class strength. However, heavy packing of eggs is most likely to occur when a large stock spawns during a short period in a restricted area. During the period 1959–1965 the spawning within areas 08, 07 and 06 was more extensive and prolonged in 1959 than in 1962 (Table 14).

The hypothesis of critical periods during early larval development expounded by Hjort (1914, 1926) has been discussed by several authors (e.g. Marr 1956, Wiborg 1957, Farris 1960, Beverton 1962, Gulland 1964, Hempel 1965). Marr concluded that although catastrophical

mortality rates will always remain as a possibility, evidence points towards survival at a constant rate or at a constantly increasing rate, rather than towards the existence of critical periods. GULLAND suggested that mortality is very high just after hatching, and that this is common to all year-classes. Then there is a density-dependent phase in which mortality is higher for year-classes with an initially high number of eggs than for one with an initially low number of eggs. According to GULLAND there is then a phase during which the strength of a year-class is determined, i.e. the phase during which the mortality of an ultimately poor year-class is higher than that of an ultimately rich year-class. Investigations by SOLEIM (1942) indicated a heavy mortality of larvae when the yolk was resorbed. DRAGESUND and NAKKEN (1968) estimated a larval mortality of 94% between a size of 10 mm and a size of 12 mm in 1967. It is likely that such a high mortality at this stage affected the abundance of 0-group herring observed in autumn of 1967 (ANON. 1967). However, comparable larval mortality data for other years are not available. Therefore, it is not possible to estimate the influence of early larval mortality on variations in year-class strength.

The extremes among the year-classes of Norwegian herring spawned during the period 1959–1965 were the rich one of 1959 and the poor ones of 1962 and 1965. Investigations carried out during the 0-group stage (DRAGESUND 1970) showed a considerably higher abundance of the 1959 year-class than of those produced in 1962 and 1965. These results suggest that the mortality of the progeny during the first six months of life may have been considerably higher for the two latter year-classes than for that of 1959. Indication was found that the variation in the size of the spawning stock was reflected in the larval abundance estimates just after hatching (Fig. 19A) and it is, therefore, unlikely that any marked difference in mortality existed before hatching of these year-classes.

When the larvae have resorbed their yolk sacs, suitable food must be available if mass mortality is not to occur. Larvae with poor swimming performance and small field of vision can only search a small volume of water (ROSENTHAL and HEMPEL 1968). For larvae with better vision and better swimming performance, which again is a function of the length of larvae, the volume of water searched every day is far greater. This factor may cause serious competition among larvae during a period of low abundance of food. ROSENTHAL and HEMPEL concluded that the very young larvae are more endangered by malnutrition than somewhat older and larger larvae because they require a higher abundance of food. This feature is in line with the hypothesis of a critical phase of starvation after the yolk stage, and supports the assumption that a restricted and concentrated distribution of larvae just after hatching is disadvantageous.

Advantageous conditions for a high survival of larvae, therefore, should exist when the larvae are dispersed in areas of abundant food supply.

According to Bjørke (1968) eggs of *Calanus finmarchicus* constituted 93% of the number of particles in the gut content of larvae investigated in 1967 off Møre during a three-week period from the time of hatching. Lie (1965) found that spawning of *Calanus finmarchicus* at Sognesjøen started in the first half of March in 1959, whereas the spawning in 1962 started later, probably in early April. Thus, the spawning of *Calanus* occurred earlier in relation to the hatching of herring larvae in 1959 than in 1962 (Fig. 28). The spring spawning of *Calanus* is followed by an increase in the zooplankton biomass. In 1962 the mean total volume of zooplankton at Sognesjøen in April and May was considerably lower than in 1959, indicating less available food for herring in 1962. On the other hand, no such differences either in time of spawning or in total plankton volume were found between the two seasons at the Skrova and Eggum stations in the Lofoten region (Lie 1965). However, these stations are located farther north of the areas where the main concentrations of herring larvae at yolk resorption were observed than Sognesjøen is located south of these areas. In 1965 the spawning of *Calanus* took place in February–March at the Sognesjøen station (Lie 1966) and the hatching of herring larvae off Møre occurred during the second half of March (Fig. 28). The hatching of herring larvae off Lofoten occurred relatively early in 1965 (about 20 March). The spawning of *Calanus* took place in March–April (Lie 1966) and it is possible that the coincidence in time between the *Calanus* spawning and hatching of herring larvae in 1965 may have been unfavourable.

The importance of abiotic factors, as for instance wind direction and force influencing year-class strength, have been stressed by several authors (Sette 1943, Carruthers *et al.* 1951, Hill and Lee 1957, Bakken 1966). Hill and Lee suggested that there was a positive correlation between rich year-classes of Arctic-Norwegian cod and strong southerly wind during the period when the larvae drift from the Lofoten spawning grounds to the Bear Island area. A similar relationship was found for herring larvae. The northward drift of larvae is hampered in years with relatively weak winds or prevailing westerly and northerly winds. This feature has probably added to the effect of a concentrated spawning in 1961 and 1962, resulting in a relatively restricted distribution. In 1961 a rather rapid northward drift took place on the southern spawning grounds just after hatching, whereas farther north the wind had a diminishing effect on the northward larval drift and led to a concentrated distribution. In 1959, 1960, 1963 and 1964, spawning took place over a wider area and the prevailing southerly winds during and just after hatching resulted in a

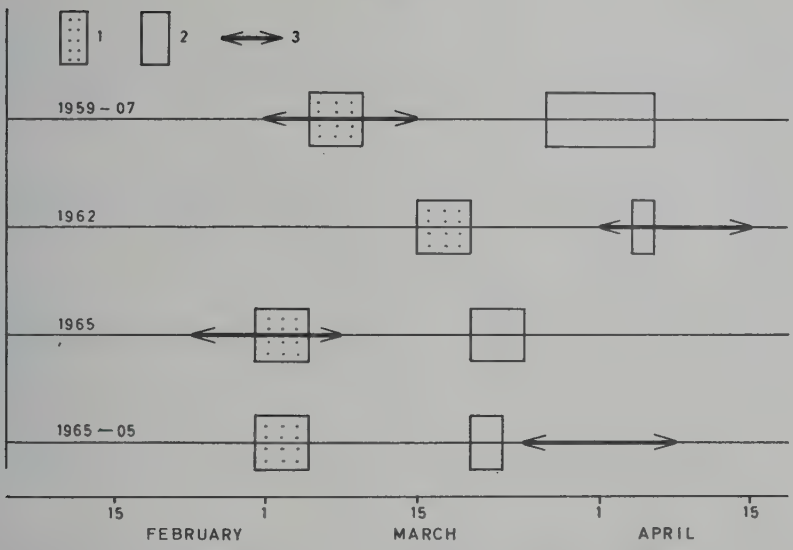

Fig. 28. Time of, (1) main spawning and (2) main hatching of herring compared with (3) time of the first spawning of *Calanus finmarchicus* at Sognesjøen (area 07) and off Eggum (area 05) in 1959, 1962 and 1965.

rapid dispersion of larvae from the spawning grounds. Also, the long duration of the spawning in these years added to the effect of southerly winds and resulted in a dispersed distribution.

Benko and Seliverstov (1968) and Postuma (1968) concluded that the water temperature during the larval and postlarval periods is an important factor controlling the success or failure of recruitment. Benko and Seliverstov found a positive correlation between the surface temperature during the larval stage and the year-class strength of Norwegian herring for the period 1948–1965. The underlying mechanism of the effects of temperature on larval mortality is complex. Temperature affects metabolic rate, i.e. incubation time, rate of growth, rate of resorption of the body reserves, swimming speed, food demand, etc. (Beverton and Holt 1957, Hempel 1965). It also affects the abundance and species composition of food plankton and predators. If the larvae are distributed in water with a relatively high temperature immediately following hatching, they may pass rapidly through critical stages. Nakken (1966) has shown a positive correlation between high temperatures in the coastal water and the current velocity. The relatively high temperatures found off Ona, Sula (near Nordøyane) and Myken (near Træna) in March and April 1959 and 1960 and partly in 1961, 1963 and 1965 (Benko and

Table 14. Summary of factors considered to be of importance in determining year-class strength of Norwegian herring compared with abundance estimates obtained at the 0-group stage and at six years of age for the 1959–1965 year-classes.

Factor	Area	Spawning year						
		1959	1960	1961	1962	1963	1964	1965
Spawning stock size in mill. tons (Fig. 2)	07 06	5.5	4.5?	3.5?	2.5	2.9	4.2	7.3
Mean age of spawning stock (Table 6)	07	9.5	10.3	10.7	11.7	12.2	8.7	7.8
	06	9.5	—	—	11.7	11.6	—	5.4
	05	—	—	—	—	3.9	4.9	5.7
Extension of spawning area, indicated by number of rectangles, where herring in spawning and spent condition were caught (Table 8)	08	2	0	0	0	0	0	0
	07	8	8	6	4	5	5	5
	06	9	9?	5?	7	6	7	9
	05	?	?	?	?	5	5	6
Approximate northward displacement (in nautical miles) of spawning centres, reference year 1959 (Fig. 3)	07	Centre: Off Stad	30	60	60	70	90	90
	06	Halten-Sklinna	0	0	0	0	0	0
Duration of spawning season in days (Fig. 4)	07	30	30	30	20	20	20	20
	05	—	—	—	—	10	10	20
Date of main spawning (Fig. 4)	07	5–9.3	5–9.3	10–14.3	15–19.3	10–14.3	5–9.3	28.2–4.3
	05	—	—	—	—	25–29.3	25–29.3	28.2–4.3
Spawning rate (Table 10)	07	3.8	5.9	6.3	8.7	?	5.3	5.3
	05	—	—	—	—	?	22.0	10.3
Date of main hatching (Fig. 7)	07	26.3–5.4	23–31.3	29.3–3.4	4–6.4	30.3–11.4	25–26.3	20–25.3
	05	—	—	—	—	16–26.4	15–19.4	20–23.3

Direction and relative strength of the mean wind vectors for March–April (Fig. 21)	07	20°	34°	62°	29°	325°	342°	45°
		120	60	180	50	85	55	90
	06	357°	354°	88°	91°	334°	50°	35°
		160	190	160	50	180	100	75
	05	20°	12°	135°	160°	310°	326°	5°
		130	200	130	80	75	60	20
First spawning period of *Calanus finmarchicus* (Lie 1965, 1966)	Sognesjøen	1–15.3	1–15.3	1–15.3	1–15.4	Feb.–March	Feb.–March	Feb.–March
	Eggum	—	1–15.4	1–15.4	1–15.4	April	April	April
Year-class strength at six months of age, echo abundance index $\times 10^{-3}$ (Dragesund 1970)		325.8	147.4	37.5	14.8	53.6	75.0	9.1
Year-class strength at six years of age (in mill. tons)		4.5	1.8	0.5	0.03	—	—	—

Seliverstov 1968) also may have been associated with higher velocity of the coastal current those years than in 1962 and 1965 when lower temperatures were found at these stations.

Table 14 compiles information from preceding chapters on factors to be of importance in determining year-class strength of herring during the period 1959–1965. The data indicate that within the range of observed stock size a relationship might exist between the parent stock and abundance of the resulting year-classes when favourable conditions occurred. However, in most of the years during the period 1947–1965, year-class strength was determined by a complex of other factors which completely ruled out the effect of the parent stock size. The following factors are considered to be most important in determining year-class strength:

1) the extent of the spawning area;
2) the duration of the main spawning season;
3) the rate of dispersion of larvae from the spawning grounds;
4) the coincidence in time between the availability of suitable food and hatching of herring larvae.

In 1959, 1960, 1963 and 1964, spawning was extensive and prolonged with a rapid dispersion of larvae from the different spawning grounds. The opposite conditions existed in 1962. In 1965 spawning was extensive and in 1961 relatively prolonged, but the conditions for transport of the larvae during the period after hatching resulted in a concentrated distribution. The gradual northward displacement of the main spawning centre during the last two decades probably has increased the importance of the timing factor, since only two definitely numerous year-classes occurred during the period 1950–1965, namely those of 1950 and 1959.

SUMMARY

1. Variation in year-class strength of Norwegian spring spawning herring is analysed in relation to the structure and the size of the spawning stock, the location and the time of spawning and environmental conditions during the egg stage and the early larval development with special reference to the 1959–1965 year-classes.

2. Stock size estimates were obtained from tagging experiments, and the number of eggs spawned in each year was calculated from fecundity data in the literature. The highest figure for the stock size (7.3 million tons) was found in 1965. The stock size had its lowest figure in 1962 when it was about 2.5 million tons.

3. The location of spawning was determined from the distribution of catches of spawning and spent herring and from the distribution of newly

hatched larvae. During the period 1959–1965 the most important spawning took place off Møre, i.e. on the shelf between Stad and Grip, and mainly in depths of less than 200 m. Spawning south of Bergen was negligible except in 1959. During the entire period spawning took place off Halten and Sklinna, whereas spawning at Lofoten was more sporadic.

4. The duration of the spawning season was determined from the maturity composition of herring collected several times a week during the spawning season. Off Møre spawning was late in 1962 (15–19 March) and early in 1965 (28 February–4 March). In 1963 spawning off Lofoten occurred about two weeks later than off Møre, and in 1964 three weeks later, whereas in 1965 spawning took place about simultaneously in the two regions.

5. The time of main hatching was estimated by adding an incubation period of generally 18–24 days (depending on the temperature) to the time of main spawning. Approximate figures for the incubation periods were obtained from the literature.

6. The distribution of herring larvae during the first month after hatching was analysed for the period 1959–1965. The larvae were collected with Clarke-Bumpus plankton samplers in oblique hauls during regular surveys covering the coastal banks between Stad and Lofoten. Factors affecting larval abundance estimates are discussed, and a general description of the vertical distribution and diurnal migration of herring larvae is given. The geographical distribution of larvae was analysed in relation to the spawning grounds. The drift of larvae was inferred from subsurface drogue experiments, wind observations and drift bottle experiments. Larval length was analysed in relation to the time of spawning. During the first month after hatching the larvae were concentrated near the coast, and almost no larvae were found outside the edge of the shelf. A more concentrated distribution of larvae was observed in 1961, 1962 and 1965 than in the other years considered. The larvae are transported northward in coastal water and the force and direction of the wind play an important role in determining the distribution pattern of larvae.

7. The results indicated that within the range of observed stock sizes a relationship may exist between the parent stock and abundance of the resulting year-classes when favourable conditions occurred. However, it is likely that the year-class strength was determined by a complex of other factors which completely ruled out the effect of parent stock size in most of the years. Conditions assumed to be advantageous for the development of strong year-classes were inferred from the present and other investigations. Strong year-classes seemed to occur when a combination of the following conditions existed:

1) widespread distribution of spawning;
2) long duration of the spawning period;
3) a rapid dispersion of larvae from the spawning grounds.

In 1959, 1960, 1963 and 1964, spawning was extensive and prolonged and with a rapid northward dispersion of larvae from the different spawning grounds. In 1962 the opposite conditions existed. Spawning was extensive in 1965 and prolonged in 1961, but the transport conditions during and after the yolk sac stage resulted in a concentrated distribution pattern.

8. The coincidence in time between the occurrence of suitable food and hatching of herring larvae is assumed to be the most important environmental factor controlling year-class strength during the early larval development. The gradual northward displacement of the main spawning centre during the last decades probably has increased the importance of the timing factor, since only two definitely rich year-classes occurred during the period 1947–1965, namely those of 1950 and 1959.

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TABLES

Table I. Number of larvae below 1 m² of surface caught with Clarke–Bumpus plankton samplers in two subsequent pairs of oblique hauls off Halten in 1964.

Date	Series 1				Series 2			
	Hour	25–5 m	50–30 m	Total	Hour	25–5 m	50–30 m	Total
16.4	1730	5	0	5	1800	0	0	0
	1937	2	0	2	2005	0	0	0
16–17.4	2350	37	16	53	0020	45	30	75
17.4	0152	18	11	29	0225	27	7	34
	0400	9	4	13	0428	2	2	4
	0605	4	0	4	0730	10	0	10
	0840	3	2	5	0910	3	2	5
	1503	0	4	4	1530	2	2	4

Table II. Number of larvae below 1 m² of surface caught in oblique hauls with pairs of Clarke–Bumpus plankton samplers attached 1 m apart, off Eggum (23–29 April) and off Træna (30 April–1 May) in 1964.

Date	Series 1			Series 2		
	Hour	24–4 m	25–5 m	Hour	49–29 m	50–30 m
23.4	0115	162	290	0320	338	280
	—	—	—	0505	348	263
28.4	1105	27	50	1315	135	161
	1455	43	47	1715	67	42
	1900	69	70	2110	43	23
28–29.4	2310	69	120	0110	106	49
29.4	0310	76	64	0508	132	58
	0705	87	85	0910	134	82
30.4–1.5	2345	31	29	0105	12	11
1.5	0300	2	10	0524	0	0
	0741	10	23	0940	2	0

Table III. Number of larvae below 1 m² of surface caught in oblique hauls with Clarke–Bumpus plankton samplers close to subsurface drogues at drift station 2 off Sklinna (18–19 April, 1964), at drift station 4 off Eggum (28–29 April, 1964) and at drift station 5 off Frøya (9–10 April, 1965).

Date		Hour	25–5 m	50–30 m	75–55 m	Total
1964	18.4	1340	5	5		10
		1600	0	0		0
		1820	9	13		22
		2005	6	12		18
		2205	64	7		71
	19.4	0015	39	2		41
		0213	49	16		65
		0420	29	9		38
		0605	6	12		18
		0805	13	6		19
		1000	2	2		4
		1205	9	4		13
		1400	2	4		6
1964	28.4	0920	74	91		165
		1105	50	117		167
		1315	66	161		227
		1455	47	58		105
		1715	52	42		94
		1920	70	45		115
		2110	94	23		117
		2310	120	60		180
	29.4	0110	199	49		248
		0310	64	53		117
		0508	120	58		178
		0705	85	108		193
		0910	53	82		135
1965	9.4	1415	18	34	21	73
		1617	21	71	24	116
		1829	9	94	42	145
		2020	115	43	16	174
		2220	53	77	7	137
	10.4	0035	18	18	0	36
		0210	121	29	2	152
		0414	60	18	3	81
		0624	15	69	0	84
		0820	0	23	2	25
		1015	0	17	4	21
		1120	0	30	7	37

Table IV. Composition (in %) of the maturity stages of Norwegian herring in five-day periods during the spawning seasons in 1959–1965.

Area	Date	No.	Maturity stage			
			IV	V	VI	VII
08	1959 23–27.2	177	4.0	48.6	36.1	11.3
	28.2–4.3	89	—	9.0	85.4	5.6
	5–9.3	272	—	9.9	83.5	6.6
	10–14.3	188	—	2.1	74.5	23.4
	15–19.3	90	—	—	90.0	10.0
07	1959 8–12.2	640	8.6	89.4	2.0	—
	13–17.2	217	2.3	96.3	1.4	—
	23–27.2	264	0.8	43.8	27.7	27.7
	28.2–4.3	364	0.3	16.2	28.3	55.2
	5–9.3	90	—	15.6	32.2	52.2
	10–14.3	186	—	7.0	73.1	19.9
08 and 07	1959 8–12.2	640	8.6	89.4	2.0	—
	13–17.2	217	2.3	96.3	1.4	—
	23–27.2	441	2.0	45.8	31.1	21.1
	28.2–4.3	453	0.2	14.8	39.5	45.5
	5–9.3	362	—	11.3	70.7	18.0
	10–14.3	374	—	4.5	73.8	21.7
	15–19.3	90	—	—	90.0	10.0
07	1960 13–17.2	1182	4.8	94.9	0.3	—
	18–22.2	1039	2.1	96.9	0.9	0.1
	23–27.2	703	—	65.7	30.9	3.4
	28.2–3.3	280	—	7.9	86.8	5.3
	4–8.3	345	—	16.2	62.3	21.5
	9–13.3	308	—	0.7	96.1	3.2
	14–18.3	134	—	3.7	88.1	8.2
07	1961 13–17.2	404	18.6	78.5	2.7	0.2
	18–22.2	531	5.3	91.9	2.8	—
	23–27.2	704	4.7	83.8	9.2	2.3
	28.2–4.3	516	0.2	33.0	30.8	36.0
	5–9.3	227	—	2.7	75.3	22.0
	10–14.3	182	—	1.1	72.5	26.4
	15–19.3	46	—	4.3	45.7	50.0
07	1962 28.2–4.3	1052	5.3	94.2	0.5	—
	5–9.3	888	0.8	82.3	11.3	5.6
	10–14.3	662	—	8.0	39.6	52.4
	15–19.3	128	—	1.6	18.0	80.4
	20–24.3	112	—	0.9	4.5	94.6

Table IV (*continued*)

Area	Date		No.	Maturity stage			
				IV	V	VI	VII
07	1963	28.2–4.3	430	3.3	66.7	29.3	0.7
		5–9.3	214	2.8	7.0	71.5	18.7
		10–14.3	116	—	—	85.3	14.7
		15–19.3	974	—	0.4	65.5	34.1
		20–24.3	204	—	—	32.8	67.2
05	1963	20–24.3	77	37.7	—	9.1	53.2
		25–29.3	264	5.3	7.2	85.2	2.3
		30.3–3.4	93	—	—	—	100.0
07	1964	13–17.2	365	18.4	81.3	0.3	—
		18–22.2	461	4.8	91.3	3.9	—
		23–27.2	636	0.6	59.0	39.6	0.8
		28.2–3.3	320	0.6	22.5	53.1	23.8
		4–8.3	315	—	8.9	67.0	24.1
05	1964	28.2–3.3	82	2.4	97.6	—	—
		4–8.3	94	—	—	100.0	—
		9–13.3	95	—	2.1	97.9	—
		14–18.3	540	—	0.2	99.8	—
		19–23.3	365	—	—	99.2	0.8
07	1965	13–17.2	317	11.4	88.6	—	—
		18–22.2	404	3.5	77.2	19.1	0.2
		23–27.2	248	0.4	29.9	66.1	3.6
		28.2–4.3	205	1.0	3.4	75.1	20.5
		5–9.3	96	—	1.0	93.8	5.2
05	1965	13–17.2	95	2.1	92.6	5.3	—
		18–22.2	175	4.6	83.4	11.4	0.6
		23–27.2	94	—	2.1	95.8	2.1
		28.2–4.3	187	—	1.6	57.8	40.6
		5–9.3	92	1.1	10.9	46.7	41.3

FiskDir. Skr. Ser. HavUnders., *15*: 451–556.

DISTRIBUTION, ABUNDANCE AND MORTALITY OF YOUNG AND ADOLESCENT NORWEGIAN SPRING SPAWNING HERRING (*Clupea harengus* Linné) IN RELATION TO SUBSEQUENT YEAR-CLASS STRENGTH

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INTRODUCTION

Doubts regarding the reasons for a decreasing yield of the herring fisheries in the southern North Sea and in the Norwegian Sea during the 1950s and early 1960s have caused fishery biologists to pay close attention to problems concerned with recruitment to the fishable stocks of herring. Nursery areas have been identified, and variations in distribution and abundance of young herring in relation to subsequent year-class strength in the adult stock have been studied (e.g. Bertelsen and Popp Madsen, 1956, 1957, Dragesund and Olsen 1965, Saville 1968, Wood 1968). Growth and migration of adolescent herring in relation to recruitment to the adult stock were investigated by Cushing (1962), Zijlstra (1963), Parrish and Saville (1965) and Østvedt (1965), and the fisheries for young herring and their effects on subsequent yield of the adolescent and adult herring fisheries have been analysed by Devold (1953, unpublished), Cushing (1959), Marti and Fedorov (1963) and Parrish and Saville (1967).

Until recently little was known about the biology of the early stages of Norwegian spring spawning herring, subsequently referred to as Norwegian herring. Lea (1929) was of the opinion that most of the 0-group herring entered the fjords of western and northern Norway and were distributed in coastal waters, but at that time no attempt had been made to search for 0-group herring in the open sea. Devold (1950) showed that 0-group herring of the rich 1950 year-class were distributed far offshore in the northeastern part of the Norwegian Sea, and he suggested that only a small part of the total 0-group population entered the Norwegian fjords. This view was not shared by Marti (1956), who held that most of the 0-group herring were to be found along the coast and in the fjords of Norway.

Lea (1929) held the opinion that 0-group herring entering the fjords emigrated during the fat-herring stage (at an age of two to three years).

He demonstrated that the development from the immature fat-herring to the adult herring took place through an intermediate oceanic stage. The fat-herring which migrated from the fjords of northern Norway did not appear on the spawning grounds the following year but arrived two to four years later, having remained in the open sea during this period.

From more recent investigations (Dragesund and Hognestad 1960, Dragesund and Olsen 1965, Devold 1968, Jakobsson 1968, Anon. 1969) it can be stated that the distribution of young and adolescent Norwegian herring is widespread and ranges from the fjords of northern Norway to the open ocean of the Norwegian Sea and the Barents Sea and varies with the different year-classes.

A fishery which is of considerable importance to the population dynamics is carried out on young and adolescent herring in Norwegian coastal waters. This fishery can be divided into two components, (1) that based on the small-herring (småsild), i.e. mainly 0- and I-group fish with the former predominating, and (2) that based on the fat-herring (feitsild), i.e. I- to IV-group herring with the II- to III- group predominating. Since the industrial small-herring fishery started in the 1910–1914 period, great attention has been paid to the effects this fishery may have on the recruitment to the older age groups. Although Lea (1924) and Devold (1953) did not find any connection between the catch of small-herring and the subsequent yield of the fat-herring fishery and could not recommend any regulation of the 0- and I-group herring fishery, many Norwegian fishermen have maintained that the exploitation of small-herring affected both the fat-herring fishery and the fishery for adult herring.

Soviet scientists have seen the low recruitment to the adult stock during the late 1950s and early 1960s as a consequence of the industrial fishery on small-herring in the Norwegian fjords (Marti and Fedorov 1963). Devold (1963), however, argued that the decline of the Norwegian winter herring fishery was caused by a series of poor year-classes, which were the results of changes in environmental factors and the migration pattern and subsequent changes in the time and area of spawning. Since no clear relationship has been found between the exploitation of 0- and I-group herring and subsequent year-class strength in the adolescent and adult stocks, the Norwegian Government has so far not introduced any rigid regulation of the small-herring fishery. However, since 1963 it has been prohibited to land catches of small-herring from 1 February to 30 April consisting of more than 50% of herring below a total length of 15 cm (north of 64° N) or 16.5 cm (south of 64° N).

Comprehensive investigations of distribution, abundance and mortality of young and adolescent herring in coastal and offshore waters of

northern Norway were initiated in the autumn of 1959 by the Institute of Marine Research, Bergen, in order to examine whether the exploitation of 0- and I-group herring in the Norwegian fjords has any primary impact on subsequent year-class strength in the adult stock. In a previous paper (Dragesund 1970) spawning characteristics and environmental conditions during early larval development were analysed as factors which may have influenced the strengths of the 1959–1965 year-classes of Norwegian herring.

The aim of the present paper is to:

1) describe the distribution of the 1959–1965 year-classes during the young and adolescent phases;
2) determine when the 0-group herring, which enter the fjords in autumn, migrate from the fjords, and investigate whether 0-group herring occurring far north and east off northern Norway migrate as adults to the spawning grounds off Møre;
3) study the variations in abundance of young and adolescent herring, i.e. small- and fat-herring;
4) estimate the mortality rates of 0- and I-group herring in the Norwegian fjords.

These items are discussed in relation to subsequent year-class strength in the adult stock.

MATERIAL AND METHODS

The material includes data from acoustic surveys, tagging experiments, herring samples and catch statistics. The statistical methods applied are those given in text books of statistical analysis (Snedecor 1956, Godske 1966). Geographical names and code numbers for areas appearing in the text are shown in Fig. 1.

ACOUSTIC SURVEYS

Every autumn during the period 1959–1965 the distribution and abundance of young and adolescent herring in the coastal and offshore waters of northern Norway were studied from combined acoustic surveys and fishing experiments with pelagic trawl and purse seine (Midttun 1959, Dragesund 1959, 1961, 1962, 1964, Dragesund and Hognestad 1962, Hognestad 1963a, Olsen 1960, Anon. 1965a). More detailed investigations during the same period were carried out in the fjords of northern Norway in collaboration with the Marine Biological Station, Tromsø. Special attention was paid to the Hamarfjord–Ullsfjord–Lyngen-

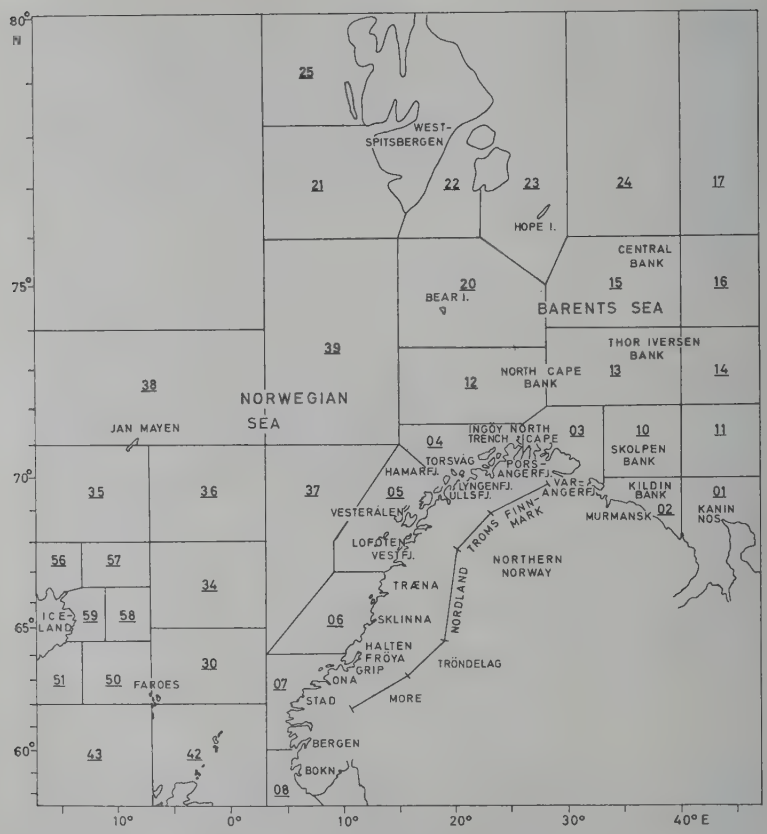

Fig. 1. Names and code numbers of areas mentioned in the text.

fjord complex and to the Porsangerfjord, and usually these fjords were investigated twice a month from September to May (Hognestad 1960, 1961, 1962, 1963b, 1964). In 1962 and 1963 observations were also made during early summer in limited regions off Troms and Finnmark, and for the years 1960–1963 information is available from acoustic surveys carried out in winter and early spring off Finnmark and in the Barents Sea (Midttun 1960, 1961, Møller *et al.* 1961, Møller 1963).

All the ships were equipped with vertical echo sounders and horizontal ranging sonars, and during the surveys the acoustic instruments were operated continuously. Except on the cruise in early summer of 1963, when the ship was equipped with a Kelvin Hughes echo sounder (MS 29,

30 kHz) and sonar (Mk2, 48 kHz), Simrad echo sounders (513–1, 38.5 kHz and 513–5, 18 kHz) and sonar (580–1, 30 kHz) were used. The sensitivity control of the Simrad echo sounders is regulated in steps from 1 to 10 and during all surveys the 38.5 kHz echo sounder was set at step 7 and the 18 kHz echo sounder mainly at step 4. In 1962 the Norwegian research vessels "G. O. Sars" and "Johan Hjort" were equipped with Simrad Research Sonar (580–10, 11 kHz), and from that year onwards a third echo sounder working on 30 kHz (580–10) was also used. However, the 38.5 kHz echo sounder has been used as standard equipment, and all the recordings have been graded according to observations made with this machine.

For every five nautical miles steamed, the echo traces of 0-group herring were plotted according to the following density classification (Fig. 2):

1) very scattered (barely visible on the recording paper);
2) scattered (the middle stages between black and white paper);
3) dense (recording paper nearly black, but with no indication of "white-line effect", which occurs when the density of the scatterers is especially high);
4) very dense (recording paper black with "white-line effect").

The most favourable conditions for estimating the abundance of herring exist during darkness when the fish are dispersed (Fig. 2, A to D) and occur as a continuous series of traces (scattering layer) on the recording paper. However, the shoaling concentrations recorded during the day (Fig. 2, E and F) were converted to night time abundance values. By frequently surveying the same area both by day and by night, factors to convert the day recordings to night time abundance values were established.

During the surveys herring were caught either with Isaacs–Kidd ten foot midwater trawl (IKMT) (Isaacs and Kidd 1953) or a larger pelagic trawl (modified capelin trawl) with headline and footline of 18.3 m, sidelines of 15.3 m and mesh size from 100 mm (wings and square) graded down to 8 mm (cod end). On some cruises a commercial herring purse seine of 8 mm mesh size was also used. Table I gives more details of the fishing experiments conducted during the surveys. In order to establish the relationship between wire angle and depth of trawling, an echo sounder transducer was attached to the depressor of the IKMT during some of the cruises, and a depth-time recorder was used on the larger pelagic trawl. The towing speed of the IKMT was usually 5–6

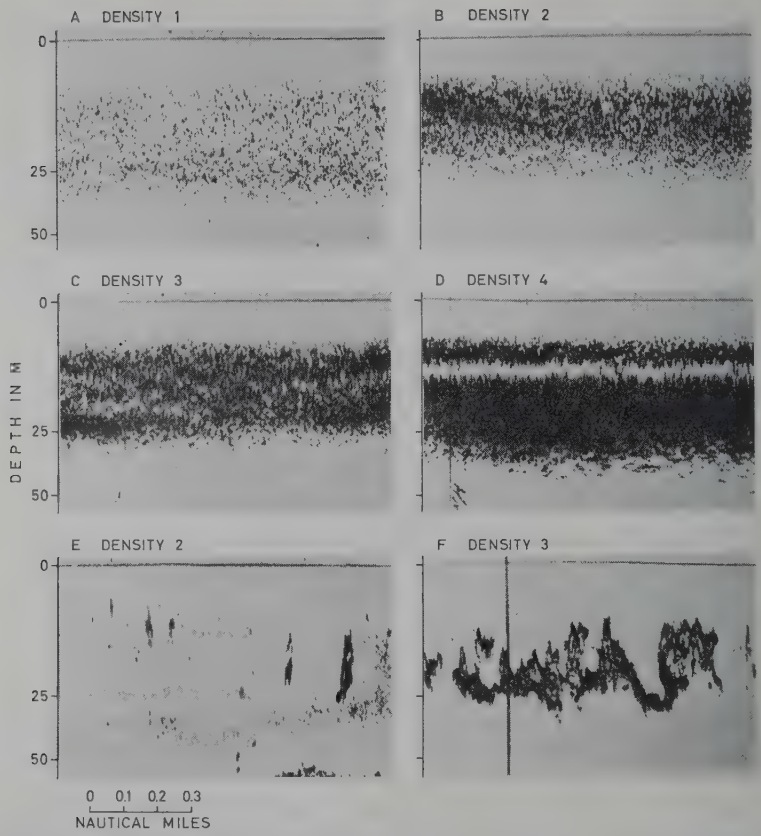

Fig. 2. Echo recordings (Simrad echo sounder 38.5 kHz set at step 7) of sound scatterers identified as 0-group herring, by night (A) to (D) and by day (E) and (F). The densities of recordings (E) and (F) are comparable with those of (B) and (C), respectively.

knots, and the larger pelagic trawl was towed at 3–4 knots. The dimensions of the pelagic trawl used by the research vessel of Marine Biological Station, Tromsø, were: Headline, 15.0 m, footline, 19.0 m, and sidelines, 4.0 m with mesh sizes graded from 50 mm to 8 mm.

IDENTIFICATION OF SOUND SCATTERERS

During the 1950s sound scatterers were frequently recorded in the top layers of water in the Barents Sea, and some success was achieved in identifying them by underwater photography (Midttun and Sætersdal

1959). However, no systematic routine programme of identification was developed until 1959. From material collected during the present surveys it has been demonstrated (Dragesund and Olsen 1965) that during late summer and early autumn 0-group fishes of different species, such as herring, cod (*Gadus morhua* Linné), haddock (*Melanogrammus aeglefinus* Linné), redfish (*Sebastes marinus* Linné), capelin (*Mallotus villosus* Müller), and long rough dab (*Hippoglossoides platessoides* Fabricius) occurred pelagically as scattering layers in the upper 100 m of water in the Barents Sea and adjacent waters.

The 0-group herring generally were found in the upper 50 m of water. During daytime they were found at depths from 25 to 50 m, while at night they came closer to the surface, dispersed and appeared as a continuous layer on the recording paper. In the daytime the herring clustered in shoals (Figs. 2 and 3). Both experimental fishing and analysis of the echo traces as well as underwater photography have been used to identify the sound scatterers during the acoustic surveys for 0-group fish. Comparisons between the IKMT and the larger pelagic trawl catches showed that the former trawl was not catching 0-group herring efficiently during the daytime and that older age groups were caught only occasionally. At night, however, when 0-group herring were distributed in typical scattering layers, they were caught frequently with IKMT. The 0-group herring were easily caught with the larger pelagic trawl both at night and day whenever they were present. The larger trawl was not reliable for catching fat-herring when these occurred in daytime shoals, but when the herring dispersed at night they could be caught with this gear. The purse seine was definitely the most reliable gear for identification of the sound scatterers, but because of the rather complicated fishing procedure involved, it was not found suitable for routine sampling. It was found necessary to identify the scatterers rather frequently, and therefore the larger pelagic trawl was chosen as the most convenient sampling gear, supplemented with the purse seine at selected stations.

When bad weather prevented fishing, identification was made from the echo traces, showing the shoaling behaviour of the fish and the difference in target strengths of the various species. By comparing the echo traces at the fishing stations with the catches obtained, it was found that 0-group capelin and long rough dab had a lower target strength than 0-group herring, redfish, cod and haddock. The four latter species, however, were difficult to separate on the basis of target strength alone. The 0-group cod and haddock were usually found somewhat deeper than the herring, and during daytime they showed a different shoaling pattern (Fig. 3, A and B). The 0-group herring formed shoals of somewhat denser concentrations and could easily be distinguished by sonar also

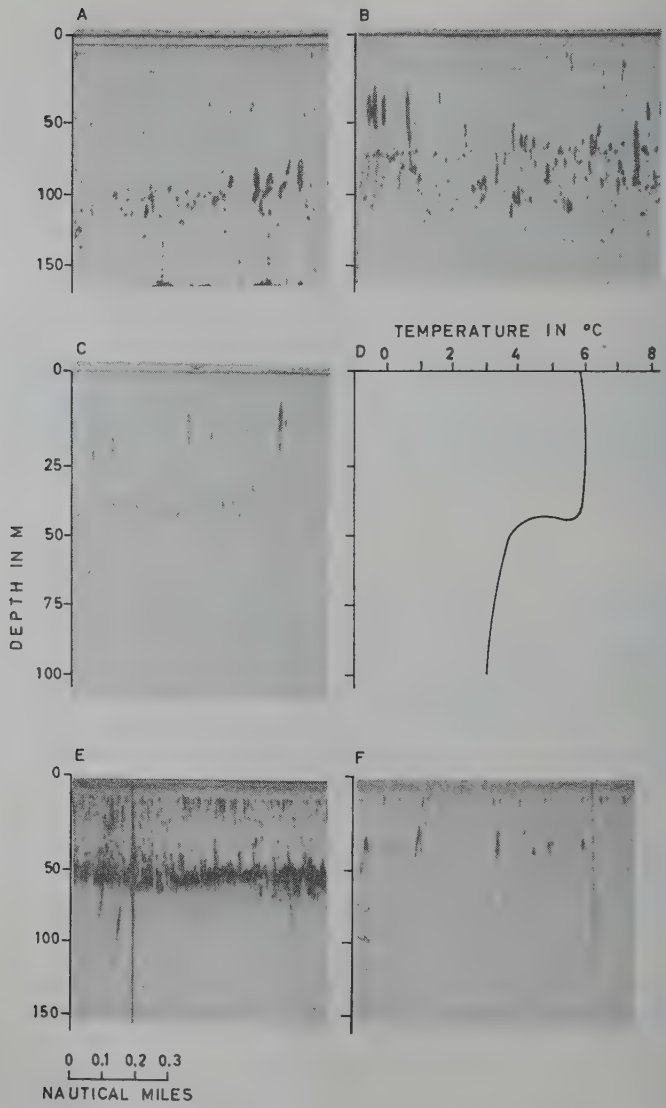

Fig. 3. Echo recordings of 0-group fish by day, (A) cod or haddock or both and (B) herring (top left) and cod or haddock (Simrad research echo sounder 30 kHz set at step—18db), (C) herring recorded above the thermocline (Simrad echo sounder 38.5 kHz set at step 7), (D) bathythermogram from the same region, (E) herring and redfish and (F) herring (Simrad research echo sounder 30 kHz set at step—18db).

when they occurred in the scattering layer together with other 0-group fishes, e.g. redfish (Fig. 3, E and F).

The shoal pattern of older age groups of herring is very characteristic and could usually be identified on the echo recordings, except in the western part of the investigated area where shoals of adult herring sometimes were difficult to distinguish from blue whiting (*Micromesistius poutassou* Risso). In such cases a distinction was made possible by increasing the resolution of the sounder by decreasing the pulse length. During early autumn fat-herring and adult capelin were rarely encountered in the same areas, while during winter and early spring fat-herring and adult capelin frequently occurred together, especially off the Finnmark coast. In this period echo recording analysis together with fishing experiments were necessary to identify the sound scatterers.

Only on a few occasions during the Barents Sea surveys was underwater photography used for identification (Midttun 1959, Hognestad 1963a, Olsen 1966), mainly because the equipment was technically inadequate for routine use. Fishing experiments combined with analysis of echo trace pattern thus have been used as principle methods for identification of the sound scatterers.

TAGGING EXPERIMENTS

Most of the tagging experiments were carried out during acoustic surveys with the R/V. "G. O. Sars", which on these occasions was equipped for purse seine fishing. The herring were tagged with internal steel tags which measured 15 ×2 ×0.5 mm for 0-group herring and 20 ×3 ×1 mm for adolescent herring. A special tagging device was developed for the small tags (Dragesund and Hognestad 1960). The large tags were inserted by means of Aasen's tagging gun (Fridriksson and Aasen 1952). The fish were taken individually from the purse seine and released into the open sea immediately after tagging. The fat-herring tagged in 1963 were obtained from commercial purse seiners, the herring being transferred to a depository net before tagging. The number of herring tagged in the different localities are listed in Table II.

Although experiments on I-group and older herring tagged with internal steel tags show relatively low tagging mortality and low shedding of tags (Fridriksson and Aasen 1950, 1952, Dragesund and Haraldsvik 1968), these factors are the most important causes of loss of tagged herring. No decisive experiments have been carried out on 0-group herring, but the experiments performed with I-group herring in tanks (Dragesund and Haraldsvik 1968) showed a tagging mortality of 10.1% and a

shedding of tags of 5.1%. These figures are used in this analysis to calculate the number of effectively tagged herring.

Nearly all tags were recovered at Norwegian reduction plants where magnets are installed for detecting the tags. The magnets were tested every autumn. The efficiency of the magnet at each factory multiplied by the quantity of herring processed gives the effective quantity of herring processed. The procedure for testing the magnets and the routine for collecting data on the catches reduced and tags recovered at Norwegian plants are described by Aasen (1958) and Dragesund and Haraldsvik (1968).

HERRING SAMPLES

In addition to samples collected during the acoustic surveys, herring samples, generally consisting of 100 specimens, were collected throughout the year from commercial catches. The herring were examined fresh, or frozen material was brought to the laboratory for examination. The weight was recorded in g. Total length was measured to the nearest half cm until January 1963. After this date, following a recommendation by the International Council for the Exploration of the Sea (Anon. 1963), the length was measured to the half cm below. A correction of 0.25 cm has therefore been added to the mean lengths of herring in samples collected after this date to make the mean lengths comparable with earlier recordings. No correction can be made for comparisons of the length frequency distributions and lengths of individual fish. The discrepancy, however, is of minor importance in the present study. Frozen herring showed a total length shrinkage of about 1.5% when compared with fresh specimens. No correction has been applied to compensate for this shrinkage.

Scales were used for age determination, and estimates of l_1, $l_2 \ldots l_n$ (the total length of a fish at the formation of the first, second, etc. winter ring) were obtained from scale measurements by using the simple proportional growth formula

$$l_n = \frac{s_n}{S} L$$

where s_n refers to measurements on the scale from the basal line to the n^{th} winter ring, S to the edge of the scale, and L is the total length of the fish (Lea 1910, Anon. 1963). Because the method of measuring the total length was changed, there is a bias in $l_1 \ldots l_n$ for samples collected after January 1963 compared with those collected prior to this date. However, back-calculations were based on the 1959 year-class, and the bias in mean annual increments for this year-class is relatively small because the mean

length of the scales ($\bar{S}$) is large compared with the mean annual increment on the scales ($\bar{s}_n - \bar{s}_{n-1}$) from 1963 onwards. Therefore,

$$\Delta\bar{t} = \frac{\bar{s}_n - \bar{s}_{n-1}}{\bar{S}} \Delta\bar{L}$$

may be almost negligible. $\Delta\bar{L} = 0.25$ cm, which is the difference between means of total lengths measured before and after January 1963.

CATCH STATISTICS

Catch statistics of small- and fat-herring of the Norwegian landings were obtained from the official fishery statistics (Anon. 1961–1962, Anon. 1963–1969). Statistics for landings by foreign vessels were derived from a report of the Atlanto-Scandian herring working group (Anon. 1969). Supplementary catch data were also recorded at reduction plants by inspectors who classified every landing of small- and fat-herring into size groups according to the number of fish per kg. Statistics on catch and participation of vessels in the small- and fat-herring fisheries also were supplied from the fishermen's sales organization, Feitsildfiskernes Salgslag.

DISTRIBUTION AND MIGRATION

RECORDS FROM ACOUSTIC SURVEYS

Young herring

The 1959 observations were the first in the present series, and the research programme had not been fully established at that time. Additional observations on the 0-group herring distribution, therefore, were procured from catch data and echo recordings of other fish surveys in the areas around Bear Island and on the western banks off West-Spitsbergen (G. Sætersdal personal communication, J. Corlett personal communication).

In the autumn of 1959 0-group herring were observed over large areas and in dense concentrations (Fig. 4). The distribution this year, therefore, is of particular interest. The concentrations of herring along the coast were generally scattered south of Vestfjord. Dense concentrations were observed particularly in the outer part of the Vestfjord, off Vesterålen and at the entrance of the fjords between Hamarfjord and Varangerfjord. At the time of the surveys only scattered shoals were found in the inner parts of the fjords of northern Norway. The records clearly demonstrated that the 0-group herring had a wide oceanic distribution with the densest concentrations in the southern part of the Barents Sea, but that they were also numerous in the northern part of the Barents Sea and towards the edge of the shelf off Bear Island.

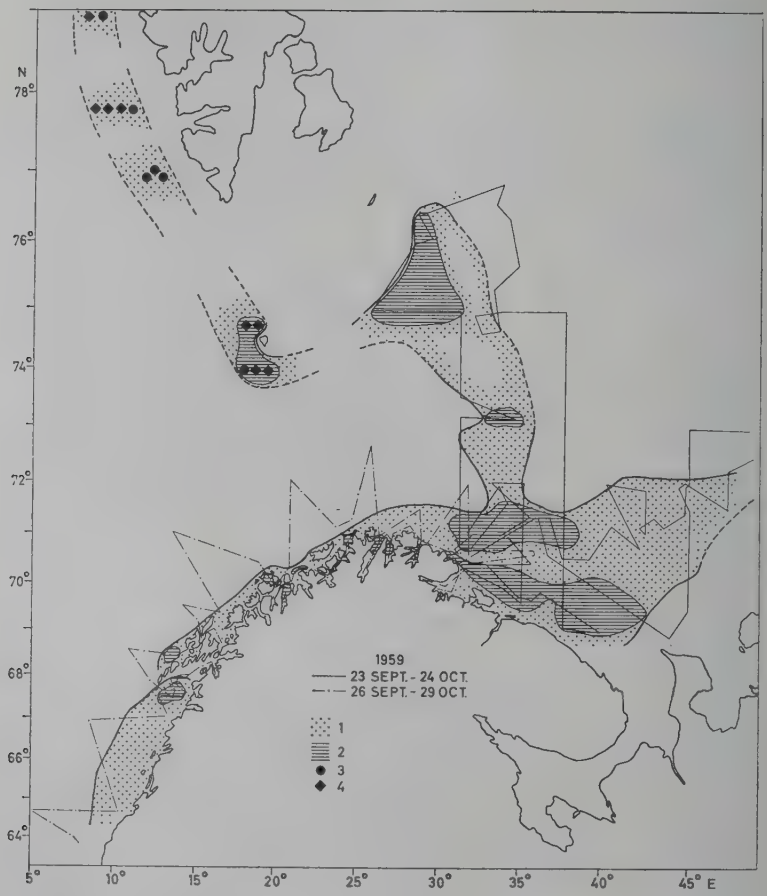

Fig. 4. Survey routes and distribution of 0-group herring in the autumn of 1959, (1) very scattered and scattered, (2) dense and very dense concentrations, (3) 0-group herring caught by bottom trawl with cover net and (4) 0-group herring identified from stomach contents of cod.

A similar pattern was found in 1960 and 1964 (Figs. 5 and 9) and partly also in 1963 (Fig. 8), whereas in 1961 and 1962 (Figs. 6 and 7) the 0-group herring were more restricted to the coastal belt. In 1965 herring were observed in two separated small regions in the open sea, i.e. between Bear Island and the Norwegian coast and along the edge of the continental shelf towards northwest of Bear Island to the southern part of West-

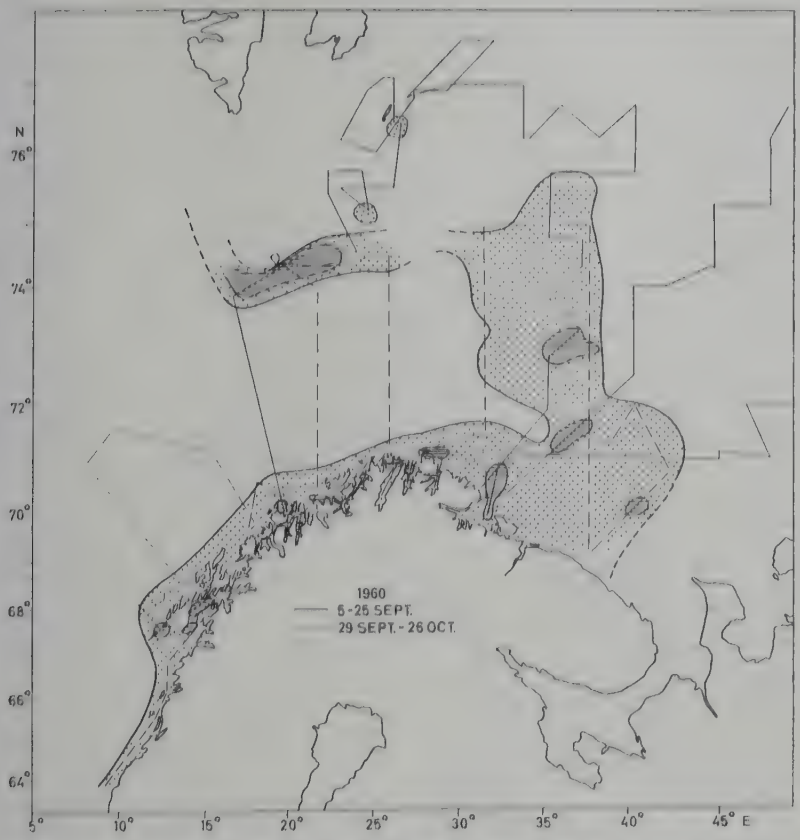

Fig. 5. Survey routes and distribution of 0-group herring in the autumn of 1960. Legend as in Fig. 4.

Spitsbergen (Fig. 10). In all the years concentrations of 0-group herring were observed along the coast, particularly at the entrances to the fjords. Between the coast of northern Norway and Bear Island 0-group herring were recorded in 1964 and 1965, but in these years the surveys were carried out somewhat earlier than in the previous years, and the herring would have moved farther east at a later date. The densest concentrations were observed in 1959, but dense concentrations were also recorded in 1960. In 1962 and 1965 the concentrations were very small.

The distribution of 0-group herring indicates that postlarval fish are transported along the path of the most important water currents off northern Norway and in the Barents Sea (Fig. 11). The herring larvae

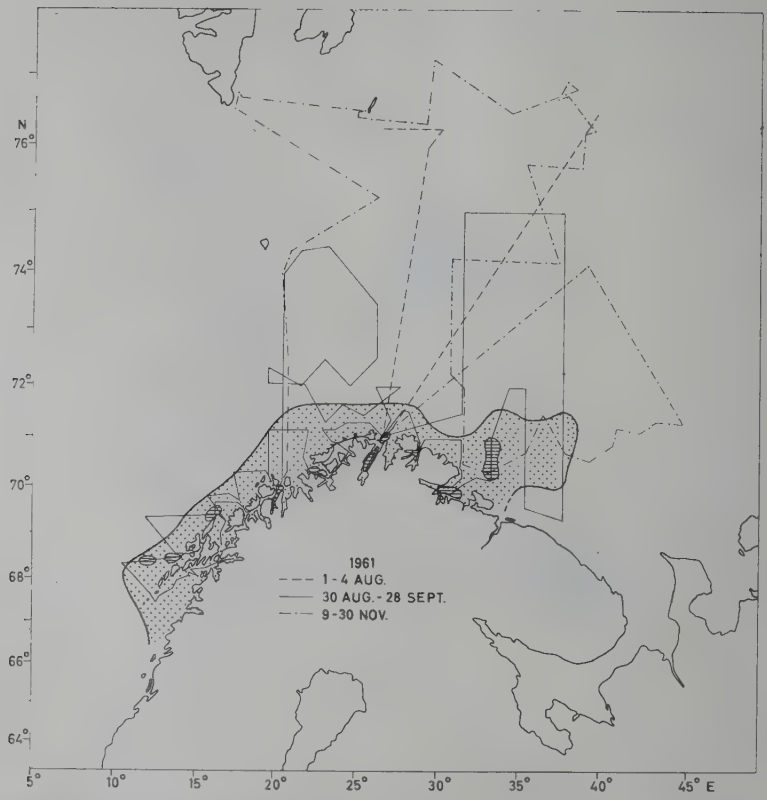

Fig. 6. Survey routes and distribution of 0-group herring in the autumn of 1961. Legend as in Fig. 4.

are transported northwards by the coastal current during the first few months after hatching (Dragesund 1970). When passing the banks off Troms, the drift of the larvae becomes more influenced by Atlantic water which in this area is intensively mixed with the coastal water (Ljøen 1962). At the entrance of the Barents Sea the water masses split into several branches (Fig. 11). One branch proceeds northwards to form The West-Spitsbergen Current, and two eastward branches separate off Torsvåg (N 70° 30′) where the shelf is wide. One of these flows along the coast of West-Finnmark (The North Cape Current) and the other continues towards the northern Barents Sea (Central Bank). The North Cape Current again splits into two branches, one along the southern and

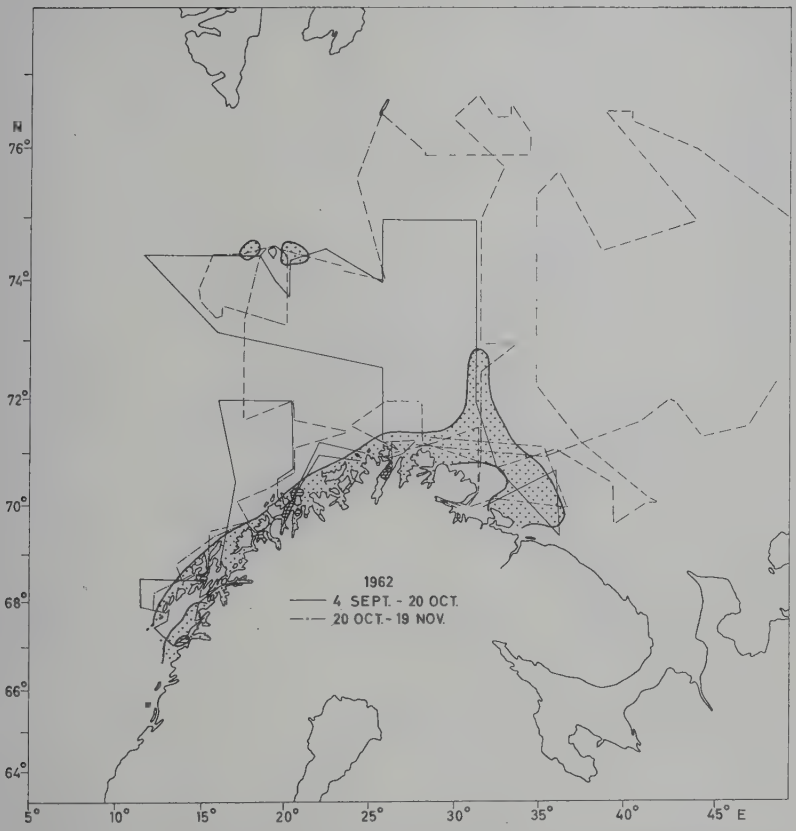

Fig. 7. Survey routes and distribution of 0-group herring in the autumn of 1962. Legend as in Fig. 4.

northern slopes of Goose Bank and the other passing near the Murman coast. Therefore, 0-group herring are always found along the coast. When the main spawning grounds are located as far north as off Møre, 0-group herring are generally more abundant on the northern than on the western coast of Norway. It cannot be determined from the present material whether the difference in distribution found between the different years was caused by hydrographic conditions during the postlarval drift phase. However, evidence was found that larvae were more widely dispersed in 1959, 1960 and 1964 than in 1961 and 1962 (Dragesund 1970). This may explain why subsequent northward drift resulted in a wide oceanic distribution in 1959, 1960 and 1964. The particularly dense concentra-

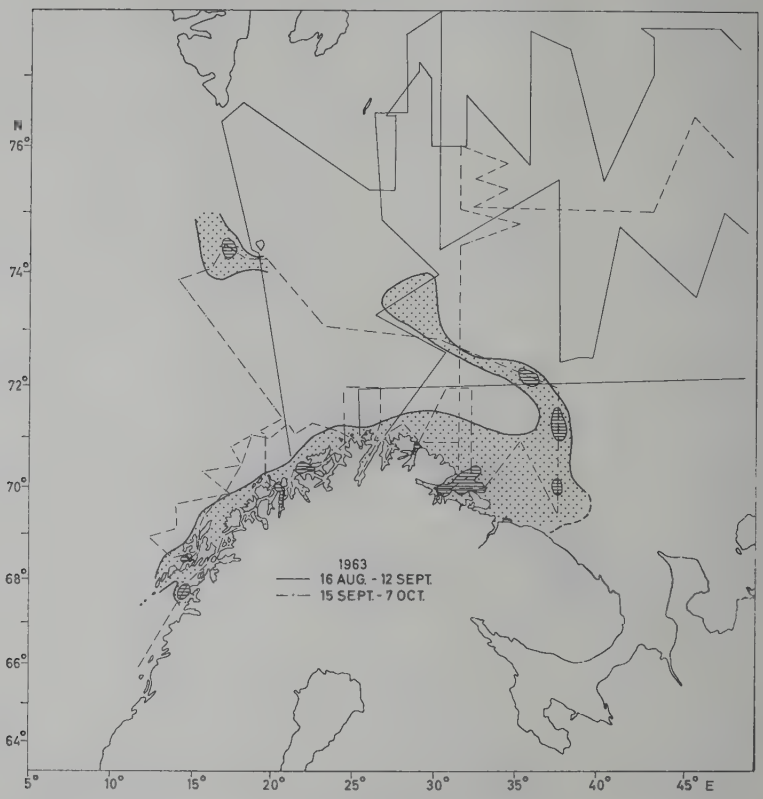

Fig. 8. Survey routes and distribution of 0-group herring in the autumn of 1963. Legend as in Fig. 4.

tions of 0-group herring in 1959 and 1960 indicated that the survival during the larval and postlarval phases was relatively high.

In late autumn a major part of the 0-group herring in offshore waters is concentrated along the fronts between the cold arctic water and the warmer water masses which cover the area west of Spitsbergen–Bear Island and the central and southeastern parts of the Barents Sea. Herring in this area will generally live in colder water during the late 0-group and early I-group stages than those accumulating along the coast and in the fjords, especially west and south of North Cape. The distribution of 0-group herring in relation to temperature is shown for the two extreme years 1959 and 1961 (Fig. 12).

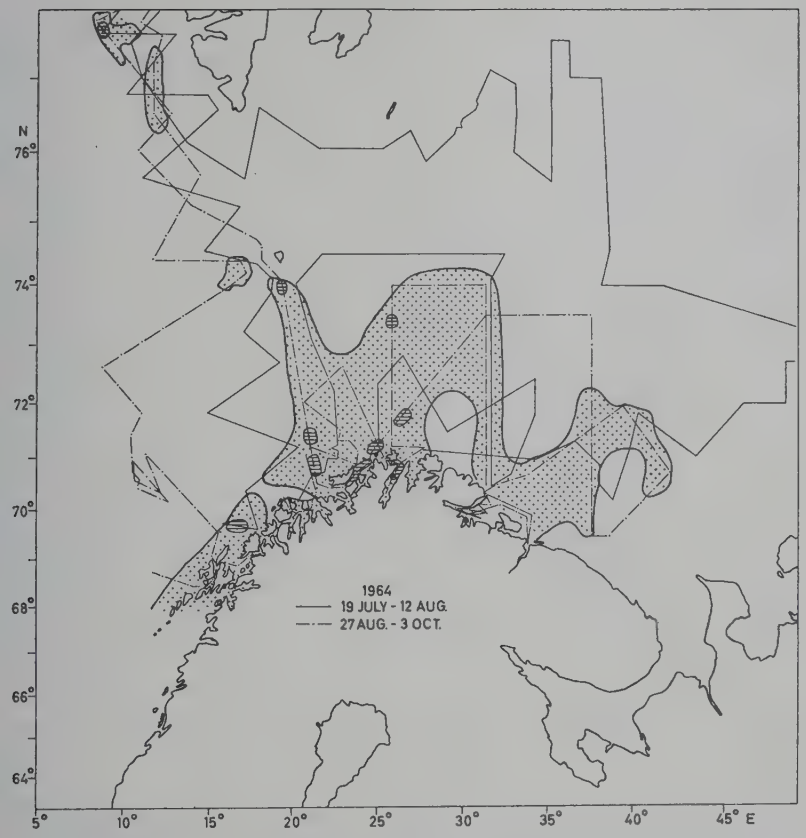

Fig. 9. Survey routes and distribution of 0-group herring in the autumn of 1964. Legend as in Fig. 4.

The herring in the northern part of the Barents Sea are mainly found in water of 1 to 4°C. In 1959 some of the herring were also found in water with a temperature as low as 0°C. In the southern part of the Barents Sea and along the coast of Finnmark, herring are mainly observed in water of 5 to 7°C. In 1961 when no herring were observed in the northern and eastern parts of the Barents Sea, the herring lived in a more uniform environment with considerably warmer water during the late 0-group stage than in 1959. This feature which may have caused a more variable growth pattern for the 1959 year-class than for the 1961 year-class, will be discussed further in a later section.

The herring accumulating at the entrances to the fjords during early

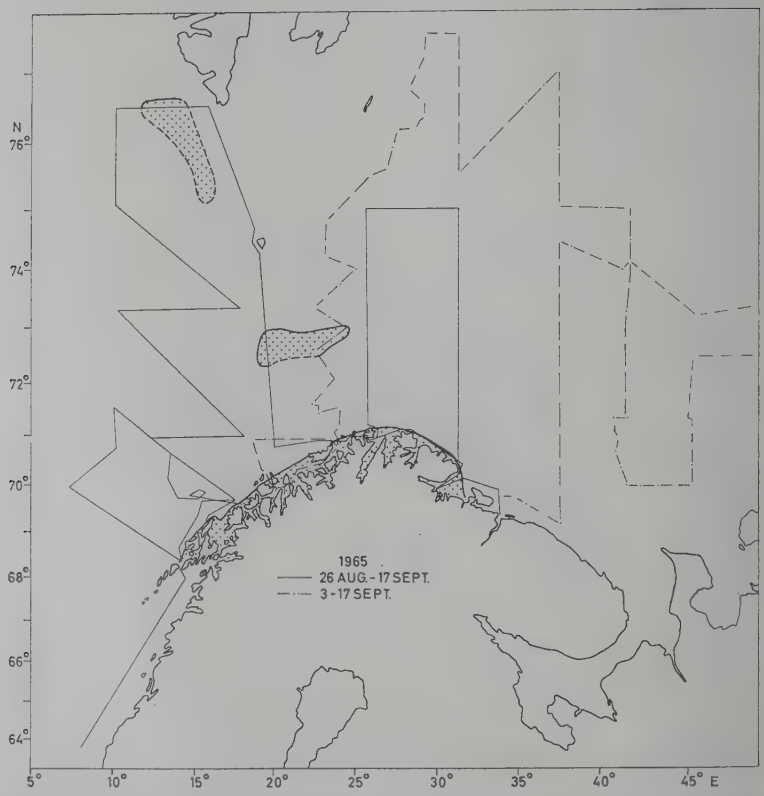

Fig. 10. Survey routes and distribution of 0-group herring in the autumn of 1965. Legend as in Fig. 4.

autumn migrate farther into the fjords later in the autumn. The situation in 1959 has been chosen to illustrate the characteristic distribution of 0-group herring during the immigration period (Fig. 13). Investigations carried out in northern Norway, mainly in the Ullsfjord region (Hamarfjord, Ullsfjord and Lyngenfjord) and in the Porsangerfjord, demonstrated that the 0-group herring remained in the fjords throughout the autumn and as I-group the following winter, i.e. the wintering period. A gradual emigration took place from March to May.

This general distribution pattern was also found in many other fjords along the coast of northern Norway. Slight variations in the behaviour during the immigration and wintering periods were found between fjords

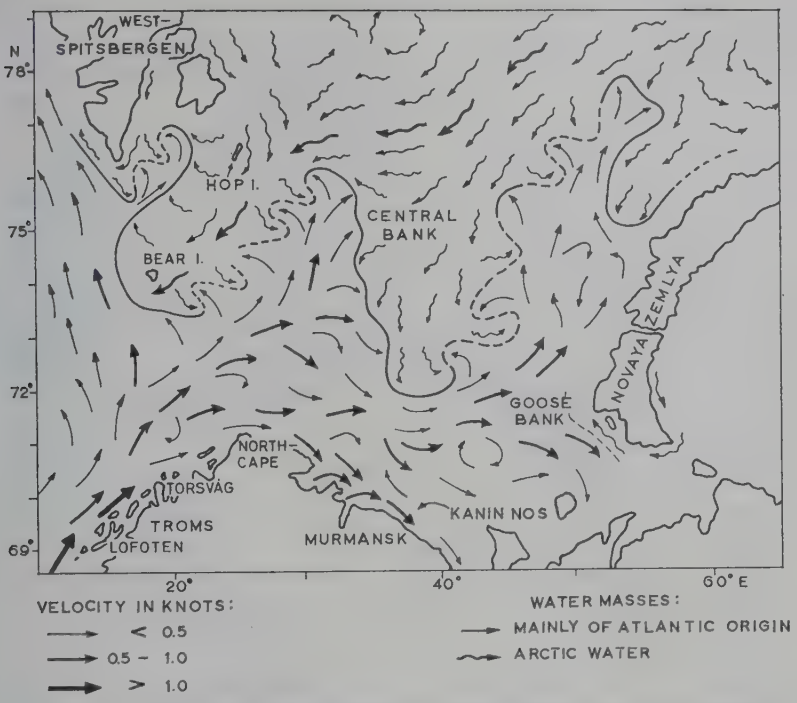

Fig. 11. General system of water currents off northern Norway and in the Barents Sea (modified from TANTSURA 1959).

and from one year to another. The Ullsfjord region in Troms and the Porsangerfjord in Finnmark were selected to study these variations. A description is given only for the wintering period from the autumn of 1959 to the spring of 1960 as this is assumed to represent the normal conditions.

In early October dense concentrations of herring were located just inside the entrance of Hamarfjord, while in Ullsfjord only few and scattered shoals were observed (Fig. 14A). During the following two weeks a further immigration took place, and in late October dense concentrations were recorded from the entrance to the central part of Ullsfjord (Fig. 14A and B). During the migration from Hamarfjord to Ullsfjord the herring were distributed at depths of 10–40 m. At night the herring dispersed, and in the day the fish clustered more closely together. During immigration, the temperature in the surface water in Ullsfjord was uniform except for a slightly lower temperature in the upper 20 m in the innermost part of the fjord (Fig. 14C).

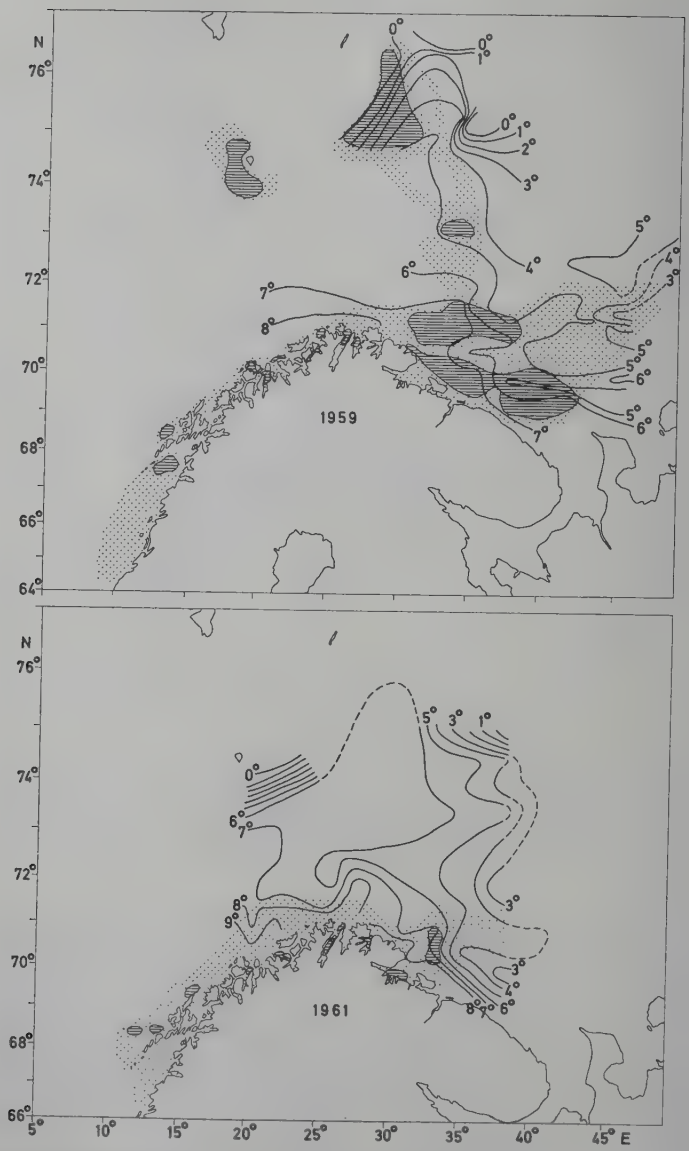

Fig. 12. Distribution of 0-group herring in relation to temperature (°C) at 50 m depth in the autumn of 1959 and 1961.

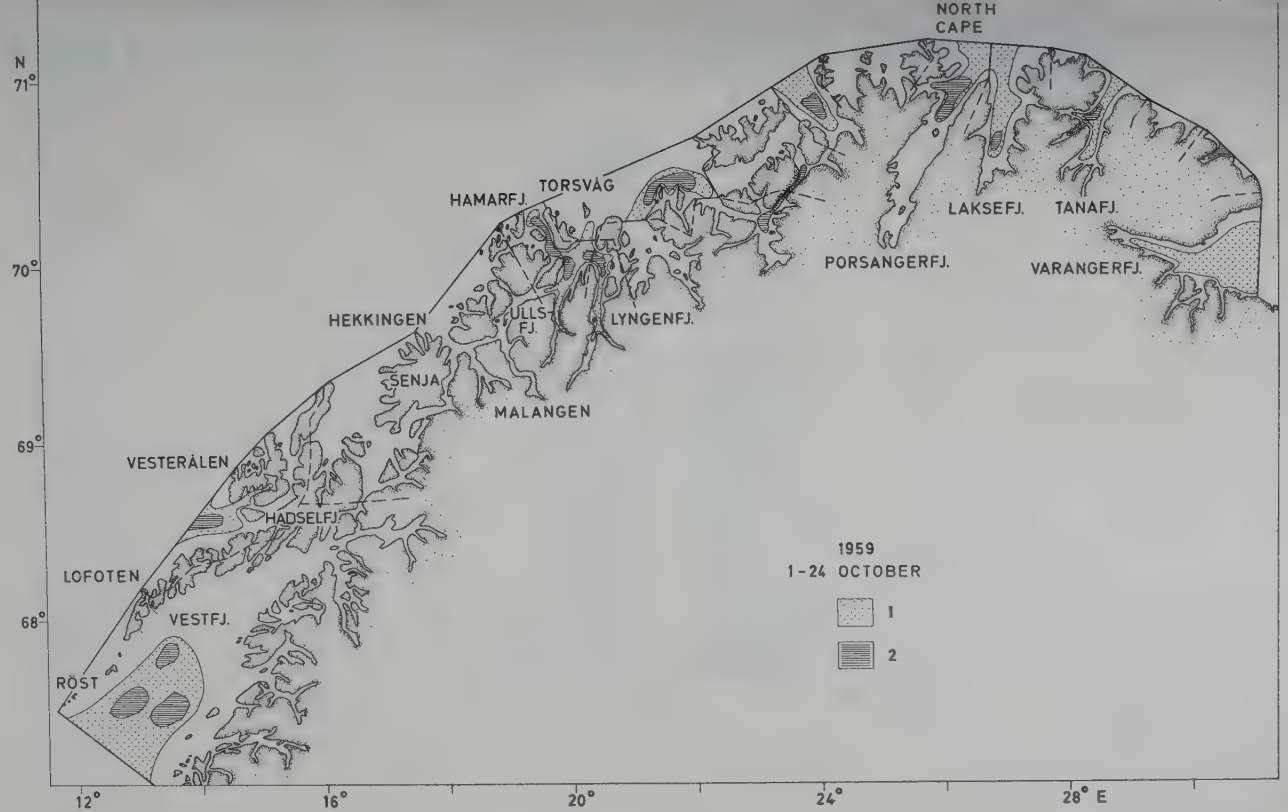

Fig. 13. Distribution of 0-group herring during the period of immigration to the fjords of northern Norway in 1959, (1) scattered and (2) dense concentrations. Herring observed inside the line drawn along the coast are later in the year subject to fishing.

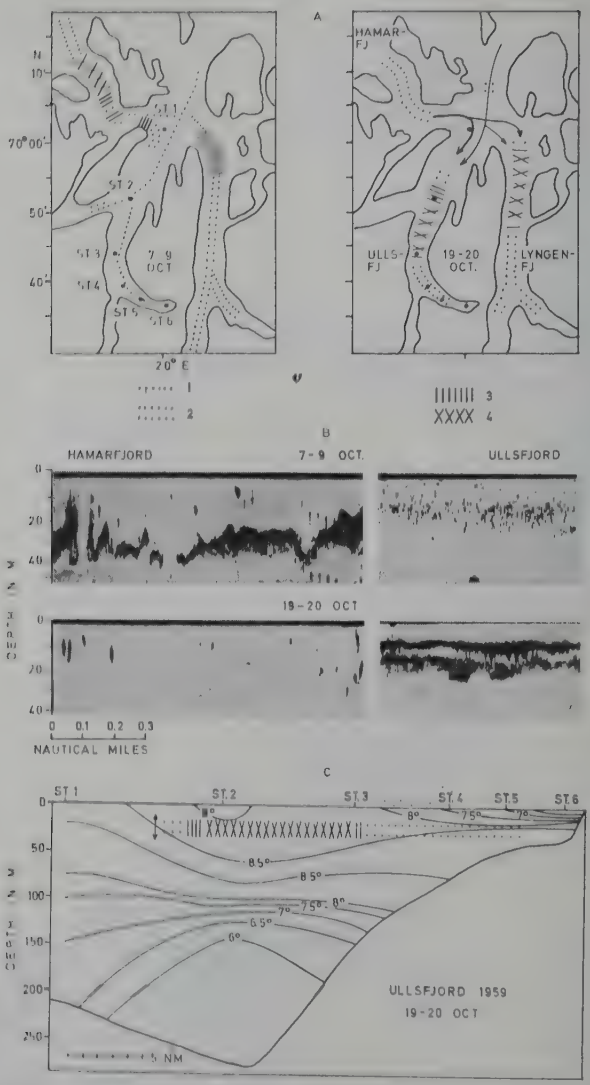

Fig. 14. Distribution of 0-group herring in the autumn of 1959. (A) in the Ullsfjord region, (1) very scattered, (2) scattered, (3) dense and (4) very dense concentrations. (B) echo recordings in Hamarfjord and Ullsfjord and (C) distribution of 0-group herring in relation to temperature (°C) in the Ullsfjord. Double pointed arrow denotes vertical extension of the distribution. Legend as in (A).

On 10 November (Fig. 15A) herring were concentrated in the inner part of Ullsfjord, and no herring were observed in Hamarfjord or off the entrance to this fjord. From October to November the fish moved from water of higher to slightly lower temperature. However, when the autumn and winter cooling started, the herring gradually moved into the central part of the fjord, where the water temperature was highest (Fig. 15B). The extent of the diurnal vertical migration increased during this period. The herring were observed near the surface at night and down to depths of 100–120 m in the daytime. In January no herring were observed in the innermost part of Ullsfjord, but herring were recorded near the surface farther out in the fjord. In February the herring were found mainly along the eastern side of the fjord and somewhat farther out. From the end of March the herring gradually migrated from the fjord, and in May the main concentrations had left the Ullsfjord region (Fig. 15C).

The migration from the entrance of Porsangerfjord and farther into the fjord started at the end of October, i.e. slightly later than in the Ullsfjord region. At that time only scattered concentrations of herring were observed outside the Porsangerfjord and in the inner parts of the fjord. The herring entered the fjord along its western shore (Fig. 16A), and from the end of November to mid-December most of the herring moved into the innermost branch of the fjord (Austerbotn), i.e. into water masses of lower temperature than those found farther out. In late autumn and throughout winter the temperature in Austerbotn was below zero, and from the end of December 1959 until April of 1960 the surface was covered with ice. The herring were found in Austerbotn when the ice broke up, and therefore probably remained in the cold water throughout winter (Fig. 16C). The emigration started in May, and the herring left the fjord within about three weeks.

A similar distribution and behaviour pattern was found for the other year-classes. The densest concentrations were observed in the autumn of 1959 and 1960, followed by 1961 and 1963. In 1962, 1964 and particularly in 1965 (Figs. 17 and 18), 0-group herring were few and scattered. In September 1965 insignificant numbers of 0-group herring were detected in the Ullsfjord region and in the Porsangerfjord. During the following two months, some small shoals migrated into the fjords. The herring concentrations were, however, more scattered than in any other year since the investigations started in the autumn of 1959.

Throughout the investigated period the immigration of 0-group herring was completed somewhat earlier in Ullsfjord than in Porsangerfjord, i.e. during the first and second half of October, respectively. In Ullsfjord the herring usually migrated to the central part of the fjord during winter, and when the winter cooling started, the extension of the

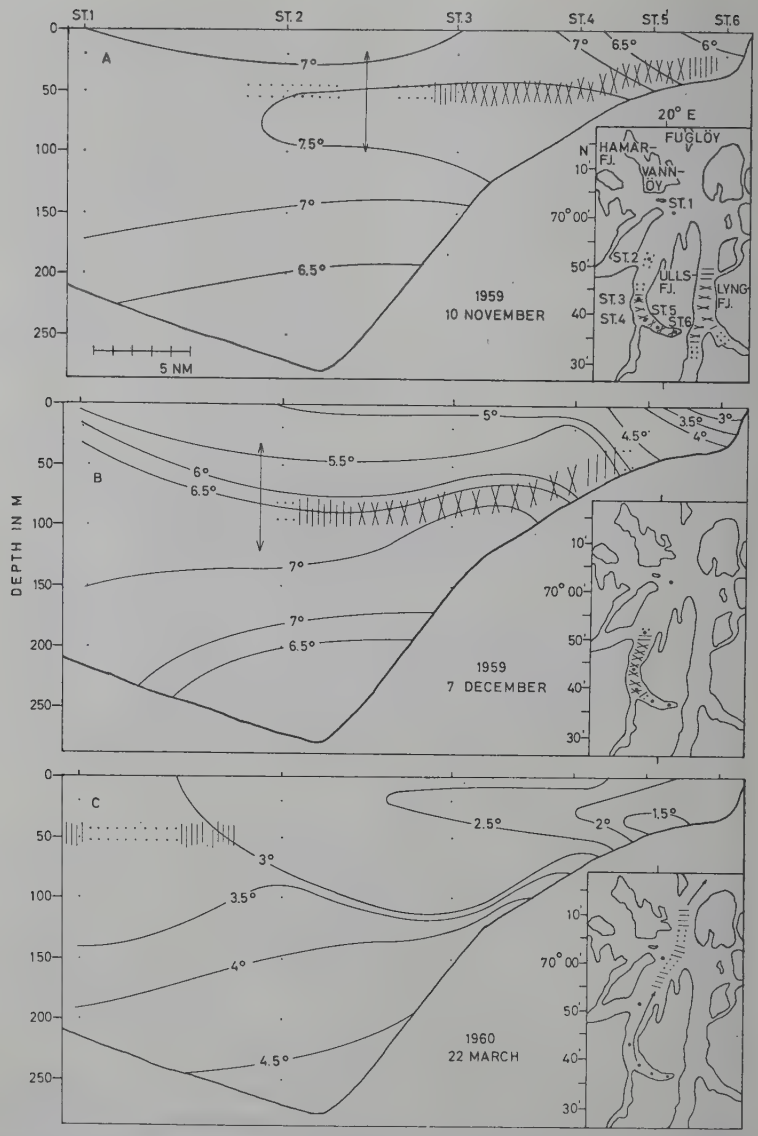

Fig. 15. Distribution of herring (1959 year-class) in relation to temperature (°C) in Ullsfjord during the wintering period 1959–1960. Double pointed arrows in (A) and (B) denote vertical extension of the distribution. Legend as in Fig. 14A.

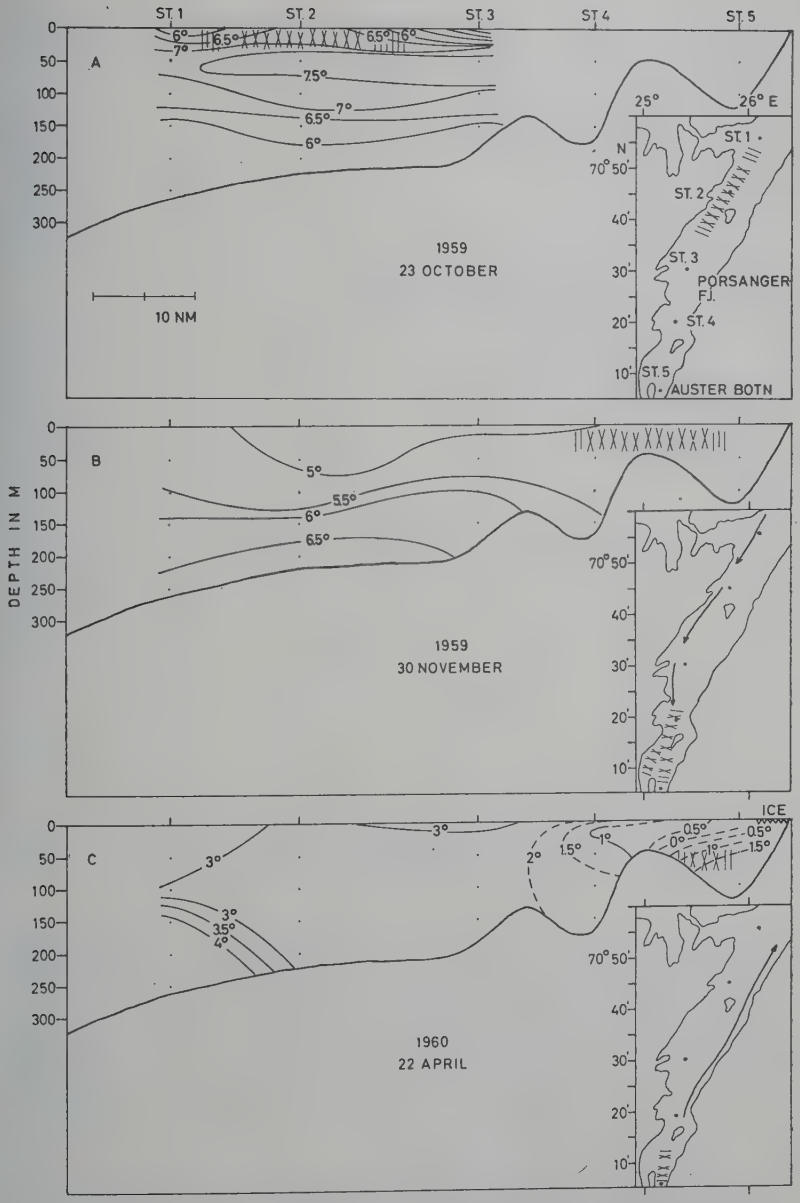

Fig. 16. Distribution of herring (1959 year-class) in relation to temperature (°C) in Porsangerfjord during the immigration and wintering period 1959–1960. Legend as in Fig. 14A.

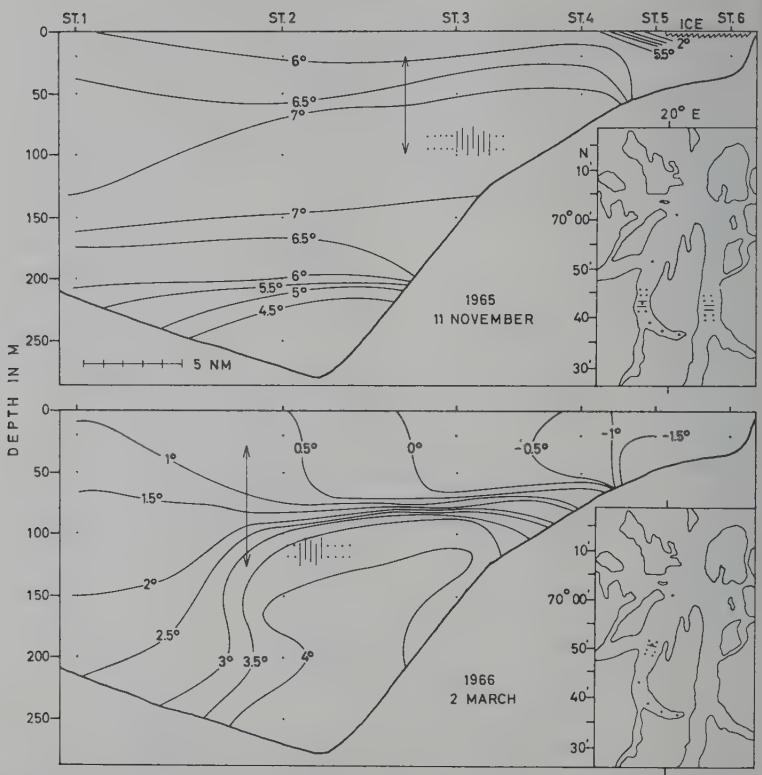

Fig. 17. Distribution of herring (1965 year-class) in relation to temperature (°C) in Ullsfjord during the wintering period 1965–1966. Double pointed arrows denote vertical extension of the distribution. Legend as in Fig. 14A.

vertical migration increased. From late afternoon to the following morning the herring were found close to the surface, i.e. above 50 m depth, whereas during the day the herring remained in the intermediate warm water layer at depths varying from 50 to 120 m. The emigration started in March when this layer disappeared, and the herring usually migrated from water of lower to higher temperature. In Porsangerfjord the herring stayed in cold water, probably near the bottom in water of temperature below 0°C, throughout the winter until May when the herring ascended and gradually started migrating from the fjord.

The fishery on 0-group herring starts with the immigration and is continued throughout the wintering period. The concentrations of 0-group herring migrating into the fjords appeared to be most dense in

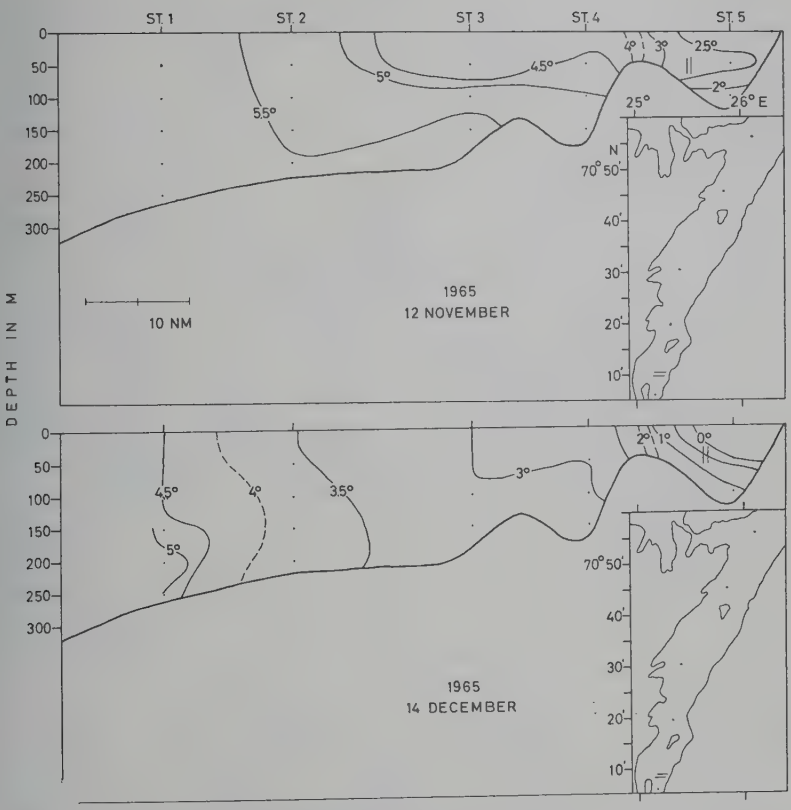

Fig. 18. Distribution of herring (1965 year-class) in relation to temperature (°C) in Porsangerfjord in November–December 1965. Legend as in Fig. 14A.

years when rich year-classes occurred, but other factors will also have an influence on the proportion of 0-group herring migrating into the fjords, e.g. the drift and distribution pattern during the larval and post-larval stages. In 1959–1960, 1960–1961 and 1961–1962 a productive small-herring fishery took place, whereas in the other years in question the fishery was rather poor, especially in 1965–1966.

Adolescent herring

The distribution and migration of the 1959 year-class during 1960 is illustrated in Fig. 19A. During winter and spring the year-class was recorded as I-group in the fjords and offshore from the banks of eastern Finnmark into the northern, central and southern parts of the Barents Sea. In Sep-

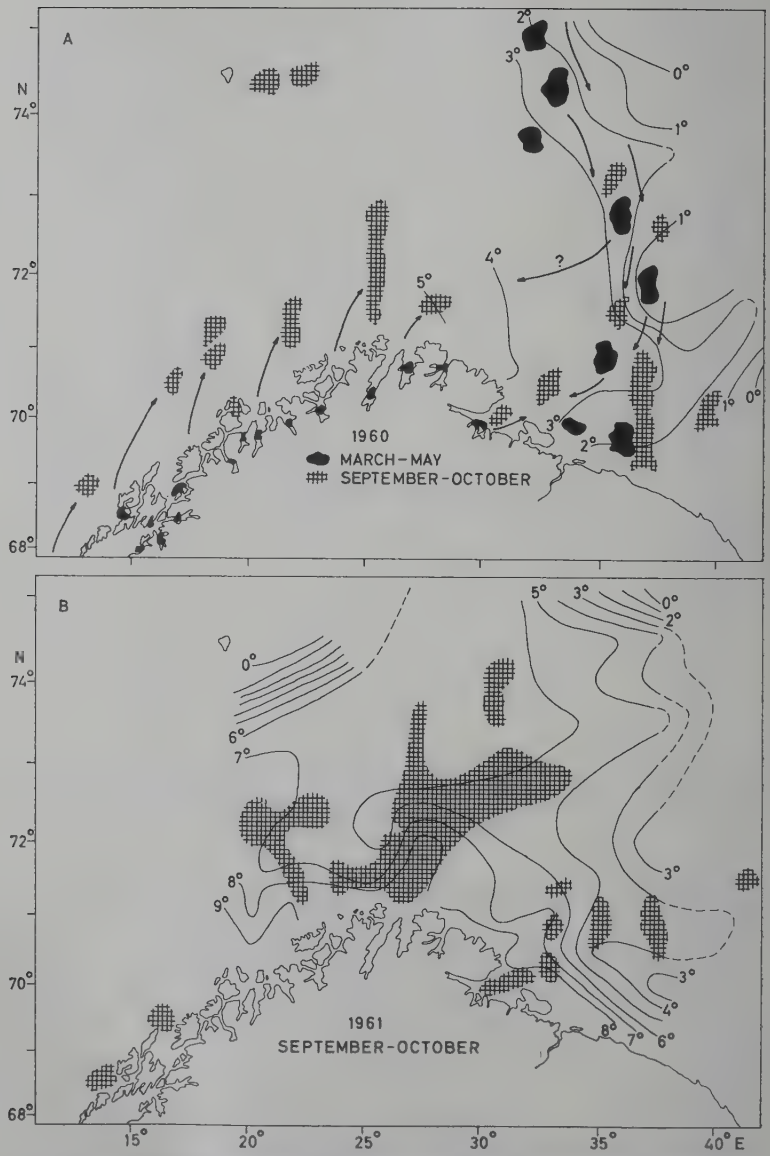

Fig. 19. Distribution of adolescent herring, mainly of the 1959 year-class in relation to temperature (°C) at 50 m depth, (A) in 1960 and (B) 1961. Temperatures in (A) refer to April—May and arrows denote the main migration routes of herring during the summer of 1960.

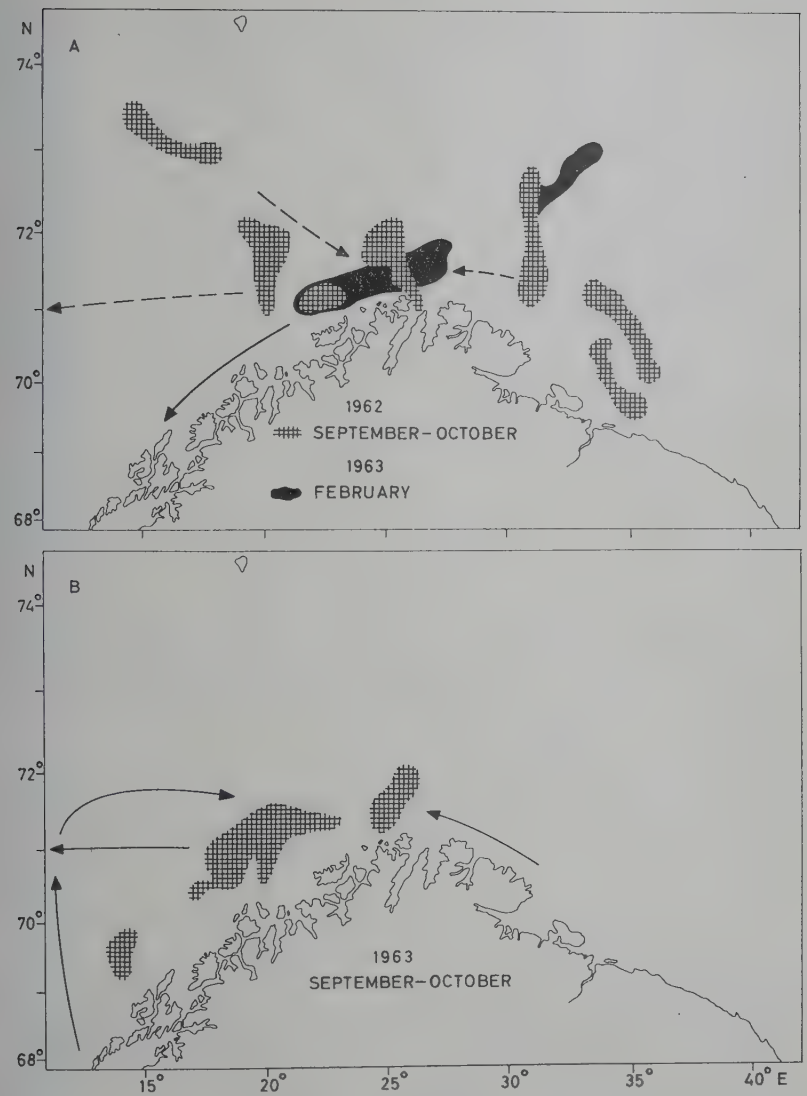

Fig. 20. Distribution of adolescent herring, mainly of the 1959 year-class, (A) in the autumn and winter of 1962 and 1963 and (B) in the autumn of 1963. Arrows indicate migration routes, broken ones summer and autumn 1962 to winter 1963, the fully drawn ones spring and summer 1963.

tember–October of 1960 the main concentrations as I-group were recorded from the North Cape Bank and eastward into the central and southern parts of the Barents Sea. During the summer of 1960 the open sea concentrations of this year-class gradually moved southward along the front between the cold and warmer water in the area from the Central Bank towards the Thor Iversen Bank. At the same time its members, which had wintered in the fjords of northern Norway, migrated from the coast. Members of this year-class also occurred on the banks around Bear Island in the autumn of 1960. Some of these herring could have wintered in this area, and others probably had migrated from the region south of Hope Island, although the majority of the herring observed south of Hope Island in the previous autumn presumably migrated southwards over the Central Bank and Thor Iversen Bank. In the winter and spring of 1961 the 1959 year-class was found in almost the same areas although the distribution was more restricted to the central and southern parts of the Barents Sea.

In the autumn of 1961 (Fig. 19B) the 1960 year-class had mixed with that of the 1959, and it was not possible to distinguish exactly between the distribution of these year-classes. However, the 1959 year-class, which was then in its third year of life (II-group), had moved farther west although it was also found in the central and southern parts of the Barents Sea. During the winter of 1962 the 1959 year-class was still observed off the coast of Finnmark and in the southern part of the Barents Sea (areas 03 and 02). The following summer dense concentrations in which the 1959 year-class predominated, were observed off Finnmark in areas 03 and 10 (Table 1).

In the autumn of 1962 (Fig. 20A) large concentrations mainly of the 1959 year-class were recorded off Torsvåg (areas 04 and 12), while other concentrations were also observed farther east. During the summer of 1962 members of the 1959 year-class migrated westwards into the Norwegian Sea, but most of the herring remained in the areas off Torsvåg. From the autumn of 1962 to February 1963 herring mainly of the 1959 year-class concentrated off western Finnmark. Some of these herring became mature and migrated later in the winter of 1963 towards Lofoten for spawning (Devold 1968). In the autumn of 1963 (Fig. 20B) most of the 1959 year-class had left the central parts of the Barents Sea and the Finnmark coast and had concentrated off Torsvåg together with herring which spawned at Lofoten in 1963.

The 1960 year-class dominated among the herring recorded off eastern Finnmark in spring and summer 1963 (Table 1). The 1963 and 1964 year-classes remained off eastern Finnmark during the entire adolescent phase (up to the end of 1968), and no westward migration could be discovered during this period (Table 1).

1. Age composition (in %) of adolescent herring caught with purse seine (PS) and pelagic trawl (PT) in some of the main fishing areas in 1961–1968.

Date	Area	Gear	No.	Year-class				
				1959	1960	1961	1963	1964
11–22.9	03 and 12	PS	215	90.7	9.3			
20.9	03 and 10	PS	97	29.9	70.1			
28.2–7.3	03 and 02	PT	102	41.2	58.8			
1.7–2.8	03 and 10	PS	973	90.6	9.4	—		
13.9	03	PT	76	57.9	42.1	—		
14–18.9	04 and 12	PT and PS	112	77.7	21.4	0.9		
6.2	04	PT	49	67.3	28.6	4.1		
2.2–5.4	03 and 13	PT	255	27.5	60.4	12.1		
4.6–25.7	03	PS	358	7.5	81.3	11.2		
1.10–28.11	04	PT and PS	725	43.2	42.2	14.6		
30–31.8	03	PT and PS	302	—	—	—	41.7	58.3
4–24.8	03	PT and PS	305	—	—	—	44.3	55.7
11.8	03	PS	50	—	—	—	36.0	64.0
8.4–8.5	03	PS	537	—	—	—	41.9	58.1

Almost all the adolescent herring found along the coast were recorded outside the entrances to the fjords. The main fat-herring fishery, therefore, took place offshore and most intensively off eastern Finnmark (area 03) and off Vesterålen and Lofoten (area 05). However, almost no fishing took place on the dense offshore concentrations recorded in the autumn of 1962 and 1963 between Torsvåg and North Cape (areas 04 and 12). During the period 1965–1968 a productive fat-herring fishery occurred off eastern Finnmark on the 1963 and 1964 year-classes which were concentrated within a relatively limited area.

LENGTH AND GROWTH STUDIES

The present investigations have shown that herring, which have wintered in the fjords during the late 0-group and early I-group stages, move into the open sea and join those which have spent their first year of life there. With increasing age more extensive migrations occur, extending into the central and western parts of the Norwegian Sea. To investigate the effect of growth on the timing of migration from the nursery areas the length and growth in different areas are compared.

Length distributions of 0-group herring are given in Table III. An analysis of variance showed in most cases significant differences in lengths of 0-group herring between areas along the coast (Table IV). However, the differences between the northernmost areas 05, 04 and 03 were not consistently significant. Mean lengths of 0-group herring in different areas

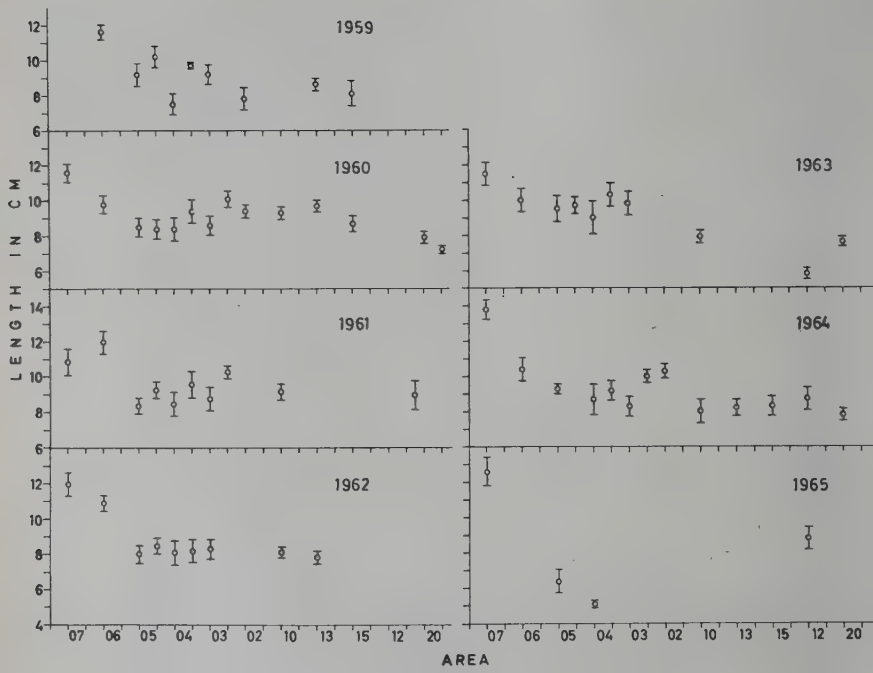

Fig. 21. Mean length of 0-group herring of the 1959–1965 year-classes in different areas. The vertical bars show the standard deviation. Samples collected with IKMT are omitted in the figure.

are listed in Table V and illustrated in Fig. 21. The mean lengths were larger for 0-group herring caught south of Lofoten (in areas 07 and 06) than for those caught north of this region. Herring collected in coastal and offshore waters north of Lofoten had variable mean lengths, but no clear decreasing trend in length was found from south to north.

Length distributions of adolescent herring of the 1959 year-class collected after the main growth seasons are shown in Fig. 22. Decreasing lengths were found from south to north. Both fast and slow growing herring were caught off Torsvåg (in areas 04 and 12). The length distribution of 3½-year-old herring caught off Iceland (areas 56, 57, 58, 59) shows that these herring had grown more rapidly than herring of the same year-class occurring off Torsvåg at the same time. The appearance of slow growing herring off Torsvåg in the autumn of 1962 (3½-year-old) gave evidence of an immigration of the 1959 year-class from the eastern part of the Finnmark coast and from the Barents Sea (Fig. 22C and E).

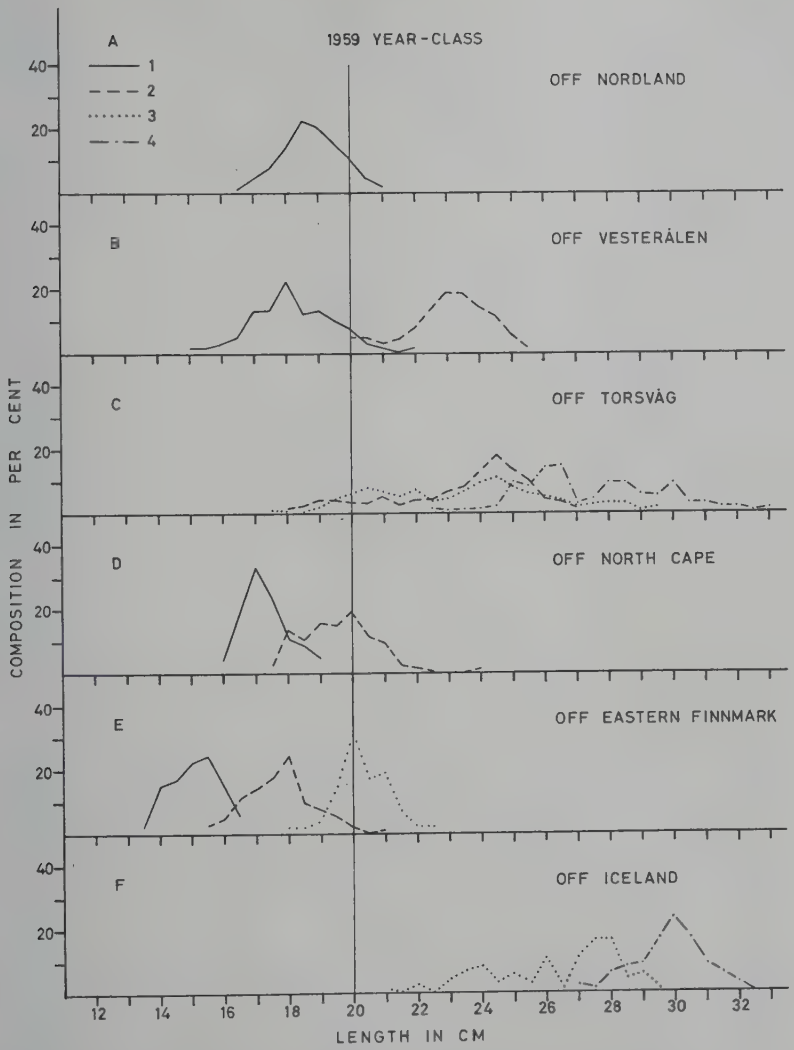

Fig. 22. Length distribution of adolescent herring of the 1959 year-class in different regions. Legend:

(1) $1\frac{1}{2}$-year-old, (A) No. = 401, (B) No. = 88, (D) No. = 49, (E) No. = 54;
(2) $2\frac{1}{2}$-year-old, (B) No. = 130, (C) No. = 176, (D) No. = 89, (E) No. = 108;
(3) $3\frac{1}{2}$-year-old, (C) No. = 244, (E) No. = 60, (F) No. = 75;
(4) $4\frac{1}{2}$-year-old, (C) No. = 142, (F) No. = 102.

Table 2. Composition (in %) of southern (S) and northern (N) growth types of the 1959 and 1 year-classes in different regions during 1961–1967. Data on the herring off Iceland are from JAKOB (1964, 1965, 1966, 1967).

Year	Region	1959 year-class				1961 year-class			
		No.	N	S	Uncertain	No.	N	S	Un cert
1961	Off eastern Finnmark	99	88.9	—	11.1				
	Off Torsvåg	100	47.0	24.0	29.0				
1962	Off eastern Finnmark	728	96.2	0.1	3.7				
	Off Torsvåg	95	91.6	—	8.4				
	Off Iceland	407	56.5	43.5	—				
1963	Off eastern Finnmark	27	100.0	—	—	40	95.0	—	5
	Off Torsvåg	309	83.2	14.9	1.9	71	31.0	47.9	21
	Off Iceland	722	54.8	45.2	—	8	—	100.0	—
1964	Off Iceland	1630	65.3	34.5	0.2	122	24.6	70.5	4
1965	Off Møre	1045	64.9	29.5	5.6	300	2.3	33.3	64
	Off Lofoten	632	82.8	12.8	4.4	51	7.8	90.2	2
	Off Iceland	2130	69.9	30.1	—	241	32.4	66.0	1
1966	Off Møre	2101	76.5	20.6	2.9	378	13.2	81.8	5
	Off Lofoten	457	85.8	12.9	1.3	84	27.4	66.7	5
1967	Off Møre	1354	80.7	17.3	2.0	374	22.7	71.4	5

Also, the relative abundance between the fast growing southern (S) and the slow growing northern (N) growth types (LEA 1929) in different regions indicates that the fastest growing members of a year-class started their westward migration towards the feeding areas in the Norwegian Sea earlier than those with a slower growth (Table 2). The 1961 year-class, which had a higher proportion of S-type herring than the year-class of 1959, showed up in catches off Iceland already in 1963 when they were $2\frac{1}{2}$-year-old.

Further knowledge of the migration pattern during the adolescent and maturing phases has been obtained from studies of annual length increments, $t_n = (l_n - l_{n-1})$. For this purpose scales from the herring of the 1959 year-class were analysed to investigate some of the characteristics of herring participating in the westward migration from the Barents Sea and the migration from the coast of northern Norway. The mean annual length increments are listed in Table VI, and the frequency distributions are illustrated in Fig. 23.

In the autumn of 1961 the main concentrations of adolescent herring were found off northern Norway, from the Vesterålen region and eastward towards the Skolpen Bank. The t_1 and t_2 distributions of herring

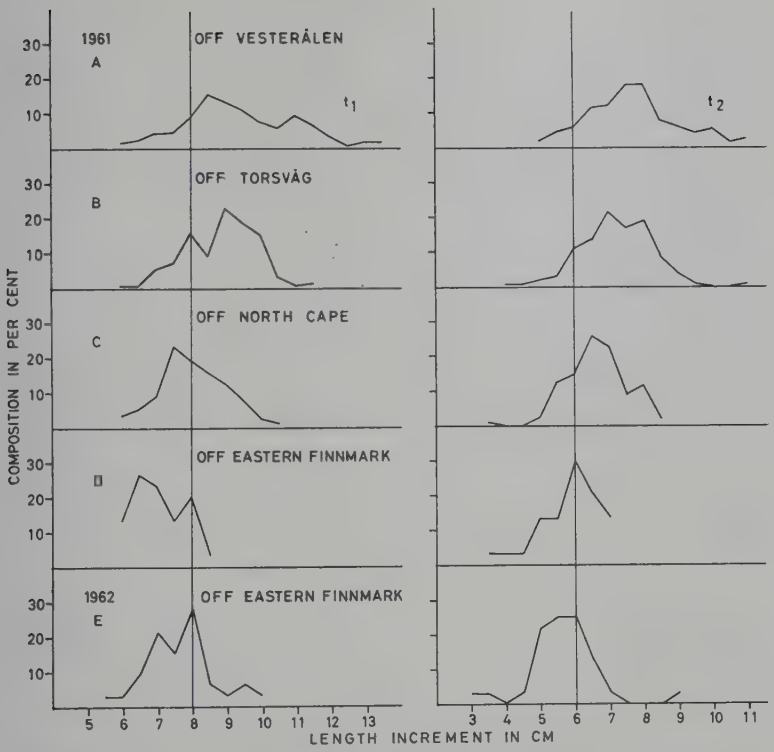

Fig. 23. Annual length increments of the first (t_1) and the second (t_2) year of life of adolescent herring of the 1959 year-class collected in the autumn and winter of 1961 and 1962.

caught in the westernmost region (Fig. 23A) show somewhat larger length increments than those off eastern Finnmark in areas 03, 02 and 10 (Fig. 23D), whereas herring collected off North Cape in area 12 and off Torsvåg show intermediate t_1 and t_2 values (Fig. 23B and C).

As indicated in Table 2 herring of the 1959 year-class appeared on the fishing grounds off Iceland during the summer of 1962. The t_1 and t_2 distributions (Fig. 24A) resemble those found off the Norwegian coast the year before (Fig. 23A), and indicate an extensive migration across the Norwegian Sea of the faster growing herring. Herring with a growth pattern similar to that found off eastern Finnmark in 1961 did not appear off Iceland in 1962.

A comparison of the t_1, t_2 and t_3 distributions of herring caught in September 1962 off Torsvåg (Fig. 24B) with those found in July farther east (Fig. 24C) suggests that herring located off Finnmark in the summer

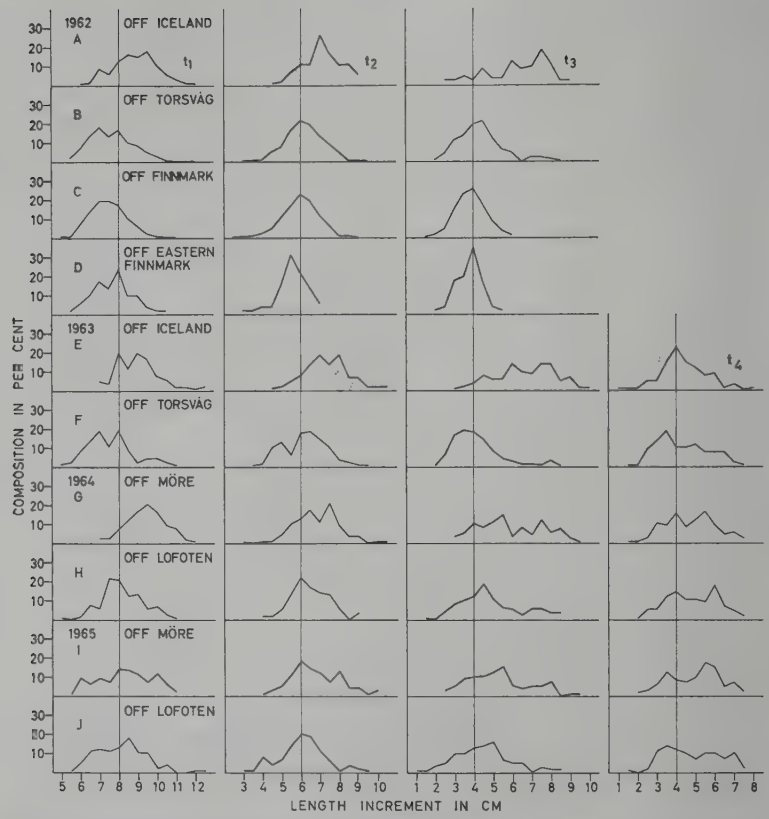

Fig. 24. Annual length increments of the first (t_1), second (t_2), third (t_3) and fourth (t_4) year of life of adolescent and adult herring of the 1959 year-class collected in 1962–1965, (A) to (F) during late summer and autumn, (G) to (J) during winter.

of 1962 migrated westward during the following months and appeared off Torsvåg in September of the same year. The length increments of herring found off Iceland in the summer of 1963 were significantly larger than those for herring caught off Torsvåg in September of the year before and in 1963 (Fig. 24B, E and F). This suggests that a westward migration into the Norwegian Sea did not take place to the same extent in 1963 as in 1962. The t_1, t_2 and t_3 distributions of herring caught off Lofoten in the winter of 1964 were similar to those found off Torsvåg in the autumn of 1962 (Fig. 24H and B), and partly also to those found off Torsvåg in 1963 (Fig. 24H and F). Herring caught off Møre in the winter of 1964 showed almost the

same length increment distributions as those caught off Iceland in 1962 and 1963 (Fig. 24G, A and E). The distribution of the annual length increments also was different for herring caught off Møre and herring caught off Lofoten during the winter herring season in 1965, although this difference, especially between the t_1 distributions, was not as pronounced as in 1964 (Fig. 24I and J, G and H).

The results of the length and growth studies show that the migration from the nursery areas is largely size determined, a feature which again probably is related to environmental conditions during the adolescent phase. The westward migration of herring spending their first year of life in the Barents Sea and off the eastern Finnmark coast was somewhat delayed, although the length distribution of the 0-group herring may be similar to that of 0-group herring spending their life farther west and south along the coast (areas 04 and 05). When the herring in these latter areas and in area 06 migrated from the coast early in the I-group stage, they joined the faster growing herring from the nursery areas in the open sea. These herring entered the feeding area in the Norwegian Sea earlier than the slower growing herring from the coastal areas and the Barents Sea.

Slower growing herring of the 1959–1961 year-classes gradually aggregated at the entrance of the Barents Sea, i.e. off Torsvåg in areas 04 and 12, during the summer of 1961, 1962 and 1963. These herring originated mainly from the fjords of Finnmark and the central and eastern parts of the Barents Sea, but also faster growing herring from the coastal areas farther south migrated to the accumulation area off Torsvåg. The fastest growing herring in this area gradually segregated from the population and migrated westwards to the central part of the Norwegian Sea and the areas off Iceland. However, some of the more slow growing herring remained in the eastern part of the Norwegian Sea throughout the summer of 1962 and 1963.

ANALYSIS OF TAG RETURNS

The migrations of herring tagged off northern Norway in 1961 and 1962 are shown in Fig. 25, and migrations of herring tagged in 1963 in Fig. 26. Both in 1961 and 1962 most of the tagged herring belonged to the 1959 year-class, in autumn 1963 the major part belonged to the year-classes of 1959 and 1960 (Table 3). Tagged herring from these experiments were recovered off Lofoten–Vesterålen and in waters off Iceland the following year. Herring tagged in 1962 and in autumn 1963 were found in catches on the spawning grounds off Møre two years after tagging, whereas herring from the tagging in 1961 did not

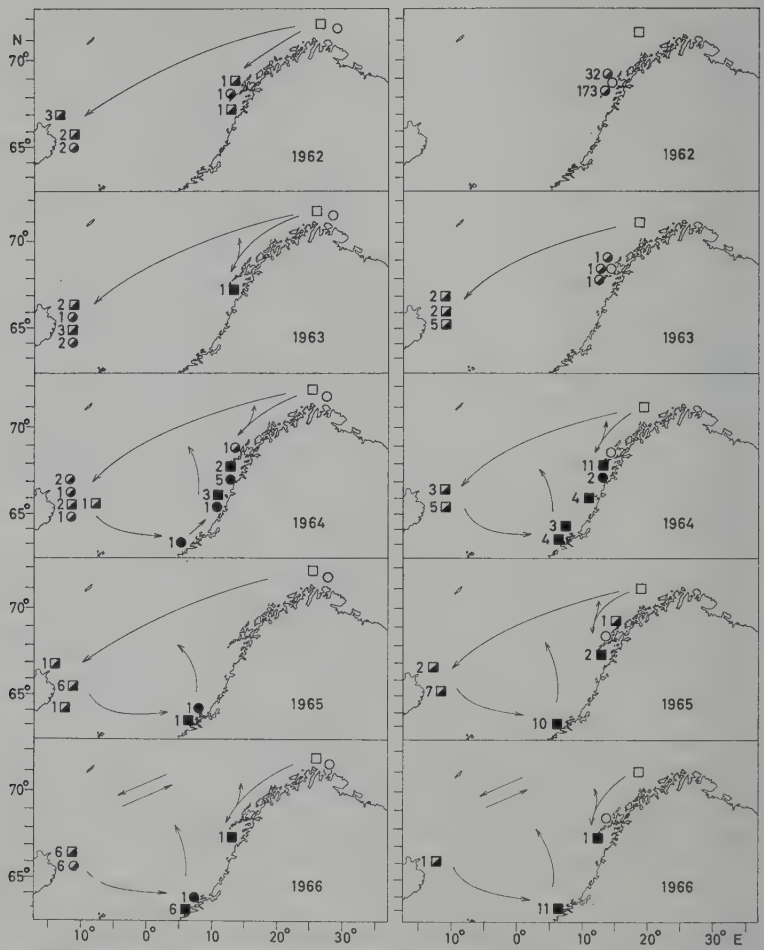

Fig. 25. Migration of herring tagged in 1961 (left column) and 1962 (right column). Open symbols indicate the tagging localities. Tags recovered during the summer fishing seasons 1962–1966 are given by half-filled symbols, recoveries during the Norwegian winter herring seasons 1963–1966, by filled symbols. The number of tags recovered is listed in the figure. Arrows indicate migration routes during the respective years.

reach these spawning grounds until three years after they were released. However, they showed up after two years in catches on the spawning grounds off Lofoten. None of the herring tagged off Varangerfjord in June 1963 has as yet (1968) been recaptured on the spawning grounds off

Table 3. Age composition (in %) of catches from which herring were taken for tagging.

Date		Tagging locality	No.	Year-class		
				1959	1960	1961
1961	12.3	Off North Cape	83	97.6	2.4	—
	22.9	Off North Cape, NE	74	94.6	5.4	—
1962	18.9	Off Torsvåg	99	83.8	12.1	4.1
	21.9	Off Vesterålen	100	1.0	3.0	96.0
1963	5.6	Off Varangerfjord	96	—	90.6	9.4
	10.6	Off Varangerfjord	99	18.2	73.7	8.1
	19.6	Off Varangerfjord	99	—	18.2	81.8
	25.6	Off Vesterålen	92	13.0	81.5	5.5
	1.10	Off Torsvåg	197	67.0	21.3	11.7

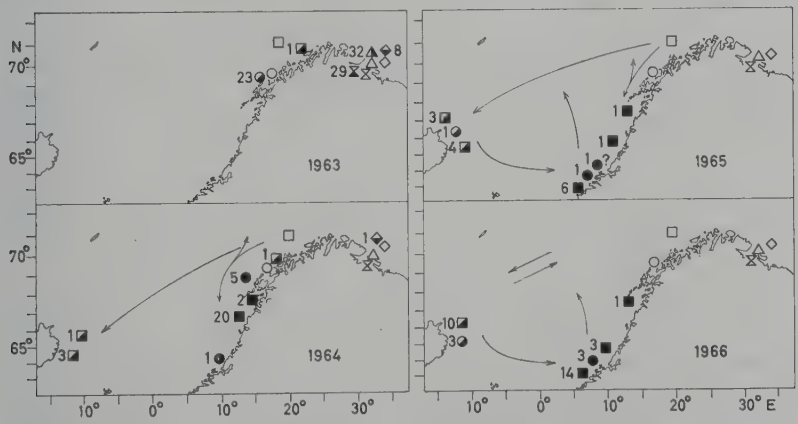

Fig. 26. Migration of herring tagged in 1963. Open symbols indicate the tagging localities. Tags recovered during the summer fishing seasons 1963–1966 are given by half-filled symbols, recoveries during the Norwegian winter herring seasons 1964–1966, by filled symbols. The number of tags recovered is listed in the figure. Arrows indicate migration routes during the respective years.

Møre or at Lofoten, but herring of the 1959 year-class tagged in autumn 1960 off eastern Finnmark (Table II) were recaptured at Lofoten in 1964 and 1966 and off Iceland in 1965.

These results indicate that recruits to the spawning grounds in the Møre region migrated via the feeding areas off Iceland through the traditional wintering area northwest of the Faroe Islands, whereas herring spawning off Lofoten remained in the northeastern part of the Norwegian Sea and moved to the Lofoten shelf from an area located off the coast of northern Norway. A more detailed description

of the migration routes for this northern component spawning off Lofoten during the period 1963–1966 has been given by Devold (1968) and Jakobsson (1968). They found that during the summer of 1966 the northern component joined the main component spawning off the Møre–Trøndelag coast, and that in 1967 and 1968 no major spawning took place off Lofoten.

It is concluded from the present investigations that herring, which in the 0-group stage were distributed far north and east off northern Norway, as adults migrated to the spawning grounds off Møre. However, this migration phase lasted longer for the herring from the northern nursery areas than for those growing up farther south. Herring from the southernmost nursery areas usually had higher growth rates and reached maturity earlier than did those spending their first years of life in the northern, central and southern parts of the Barents Sea. Accordingly, herring from these nursery areas might appear as recruit spawners from one to four years later than those from areas farther south. Taking into account the mortality during the migration phase, herring from the Barents Sea will be considerably more reduced in numbers before they reach the spawning grounds off Møre than those spending the 0-group stage along the coast south of Lofoten.

ABUNDANCE

ESTIMATES FROM ACOUSTIC SURVEYS

The distribution of 0-group herring together with the density of the echo recordings (the echo abundance) have been used to study the variation in abundance from one year to another. The surveys did not cover all the fjords. In order to obtain an estimate of abundance valid for the total distribution in inshore waters, the ratio between the area covered by the 0-group herring and the surface area in fjords which were investigated, also was applied to the fjords which had not been surveyed. In area 05 ratios for Hadselfjord and Vestfjord were used, in area 04 mainly ratios for Ullsfjord and Lyngenfjord, and in area 03 ratios for Porsangerfjord, Laksefjord, Tanafjord and Varangerfjord (Fig. 13). The total geographical distribution of scattered and dense concentrations in areas north of 67 °N was estimated for the surveys illustrated in Figs. 4–10. The estimated areas of distribution are listed in Table 4.

Fishing experiments with purse seine (two in 1960 and five in 1963) in scattering layers above 30 m depth at night were carried out to establish a conversion factor between scattered and dense echo recordings (Fig. 27). The ratio between the catches in litres taken in scattering layers (0–30 m depth) with density 1 to 2 (scattered) and density 3 to 4 (dense) was about

e 4. Area of distribution (in square nautical miles) of scattered and dense 0-group herring entrations and indices of echo abundance for 0-group herring in offshore and inshore areas in the autumn of 1959–1965.

ar-ass	Offshore			Inshore			Total		
	Scat-tered	Dense	Abund-ance index	Scat-tered	Dense	Abund-ance index	Scat-tered	Dense	Aund-ance index
59	62250	25318	315430	2520	784	10360	64770	26102	325790
60	70144	7017	140314	3599	344	7039	73743	7361	147353
61	23044	852	31564	3034	293	5964	26078	1145	37528
62	12249	—	12249	1203	132	2523	13452	132	14772
63	28312	2023	48542	2989	204	5029	31301	2227	53571
64	58700	1263	71330	2845	78	3625	61545	1341	74955
65	8400	—	8400	739	—	739	9139	—	9139

1:10. Indices of total echo abundance, therefore, were estimated by multiplying dense recordings by a factor of 10 (Table 4). The vertical extension of the scattering layers was not taken into account in these estimates.

The abundance indices for the total 0-group stock are by far the highest for the 1959 and 1960 year-classes, followed by those of 1964, 1963 and 1961. The estimates for the 1962 and especially for the 1965 year-classes are by far the lowest.

Estimates of the abundance of 0-group herring in the open sea (offshore) compared with that recorded in the fjords (inshore) have also been made for each year-class (Table 4). Not all of the 0-group herring observed along the coast migrated into the fjords. This was indicated by the low frequency of returns of 0-group herring tagged just outside the coast or at the entrances to the fjords, e.g. off Vesterålen in 1959 (Table 6). None of the 0-group herring tagged in 1960 off Bear Island and off eastern Finnmark has been recaptured in inshore areas. To separate the offshore from the inshore population, half of the area with recordings outside the border line drawn in Fig. 13 between Røst and North Cape was classified as offshore and the other half classified as inshore. Herring observed outside the fjords off eastern Finnmark are assumed not to migrate into the fjords and are included in the offshore distribution.

From Table 4 it appears that a relatively small part of the total 0-group population was distributed in the fjords in the autumn of 1959, 1960, 1963, 1964 and 1965 (3–10%). However, in 1961 and 1962 a somewhat higher percentage (15–20%) of the total 0-group population was found inshore. The results indicate that the proportion of 0-group herring entering the fjords is inversely related to the total abundance of the

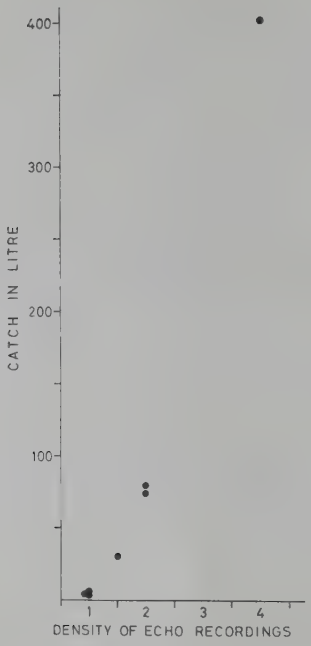

Fig. 27. Relationship between the density of the scattering layer recorded by echo sounder and the catch of the sound scatterers sampled with purse seine. The catches consisted almost entirely of 0-group herring.

0-group stock. In years when the herring are mainly restricted to the coastal belt, a relatively higher percentage of the population is found inshore.

CATCH AND CATCH PER UNIT EFFORT

Catch and effort statistics from the small- and fat-herring fishery can also be used to analyse the variations in year-class strength. The total catch of small- and fat-herring landed during the period 1930–1968 (Fig. 28), shows that considerable fluctuations have occurred. The most important small-herring fishery occurs in the fjords from late autumn to early spring, with the late autumn period being the most important. The period in the early spring coincides with the migration from the fjords. The fat-herring are usually caught at the entrances or outside the fjords, and the fishery starts in early summer and has its peak in the summer or early autumn.

In the Norwegian catch statistics herring weighing ≤ 50 g, corresponding to a total length up to 18–20 cm, are grouped as small-herring

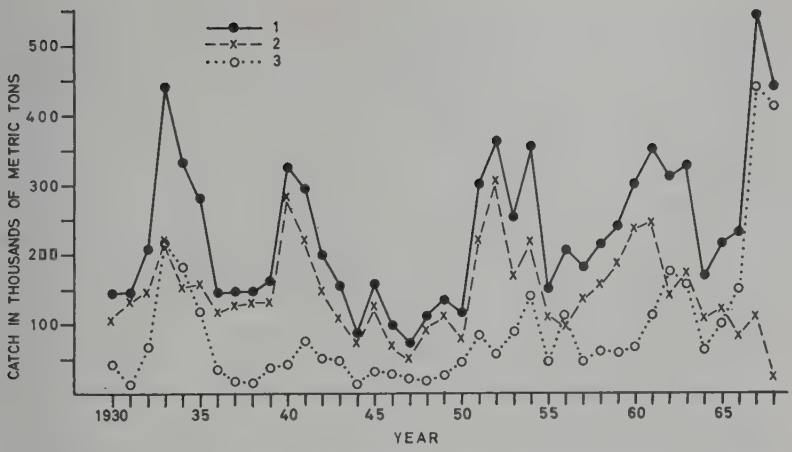

Fig. 28. Norwegian and Soviet catches of young and adolescent herring in 1930–1968, (1) total catch, (2) small-herring and (3) fat-herring.

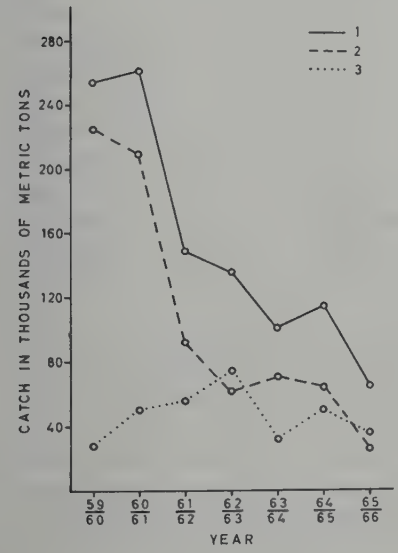

Fig. 29. Catches of small-herring landed from 1959–1960 to 1965–1966, (1) total catch, (2) 0- and I-group and (3) I- and II-group herring. Catches landed in 1959–1960 are due to the 1959 and 1958 year-classes, respectively, in 1960–1961 to the 1960 and 1959 year-classes, etc.

and fish weighing $\geq$51 g are listed as fat-herring. The small-herring subject to fishing in the autumn are mainly 0-group fish. During the following summer when these are in the I-group stage, the fastest growing herring appear in the fat-herring catches. This is especially true in areas 07, 06 and 05. The I-group herring in the northernmost areas 04 and 03,

and those with lower growth rates in areas 07, 06 and 05 are still found in the small-herring catches throughout the second year until the summer of the third year of life when they, as II-group herring, gradually appear in the fat-herring catches. With a new 0-group entering the fishery every autumn, three different year-classes are represented in the small-herring catches during a calendar year. However, during the period from 1 September to 31 August the next year the catches consist mostly of two year-classes. The catches were separated on year-class by analysing the samples collected by the inspectors at the various reduction plants along the coast (Fig. 29). During 1959–1966, the 1959 and 1960 year-classes yielded the highest catches followed by the year-classes of 1961, 1963, 1964, 1962 and 1965.

Since the small-herring are mixed with the fat-herring in the catches, it is difficult to collect samples which give a representative age composition of the fat-herring landed. However, small-herring were avoided in the samples by excluding herring weighing ≤ 50 g, corresponding to lengths less than 18–20 cm. Fig. 30 shows the age composition of fat-herring in the different areas. Most of the samples were taken during the summer and autumn. Samples collected in areas 07 and 06 during the first half of the year (1 April to 31 May) were grouped separately, and in these samples I-group fish were excluded. These herring, usually called "forfangstsild", are a mixture of young recruit spawners and fat-herring. During the period 1959–1968 the yield of the fat-herring fishery was highest in 1961–1963, when the 1959 and 1960 year-classes dominated and in 1966–1968 when the year-classes of 1963 and 1964 were dominant, with a maximum yield in 1968. Herring older than five years were only rarely found in the fat-herring catches, except during the "forfangstsild" season.

In Table 5 catches of fat-herring are separated on year-class and area. The 1964 year-class has yielded the highest catch followed by those of 1959, 1963, 1960, 1961 and 1962. An evaluation of the 1965 year-class is omitted because catch data still are incomplete. The ranking of year-classes by catch is different from that found in the small-herring catches and the exploitation rate of the 1963 and 1964 year-classes obviously has increased. A further discussion of this feature will be given in a later section.

Almost all the catches of small- and fat-herring are taken with purse seine, and the fishing fleet which is equipped with echo sounder and sonar, usually moves from one fjord to another searching for herring. Prior to 1964 the purse seine was shot from two dorries, but from 1964 onwards the power block was introduced and the purse seine, which was then shot from the vessel, was gradually made deeper. Accordingly, the

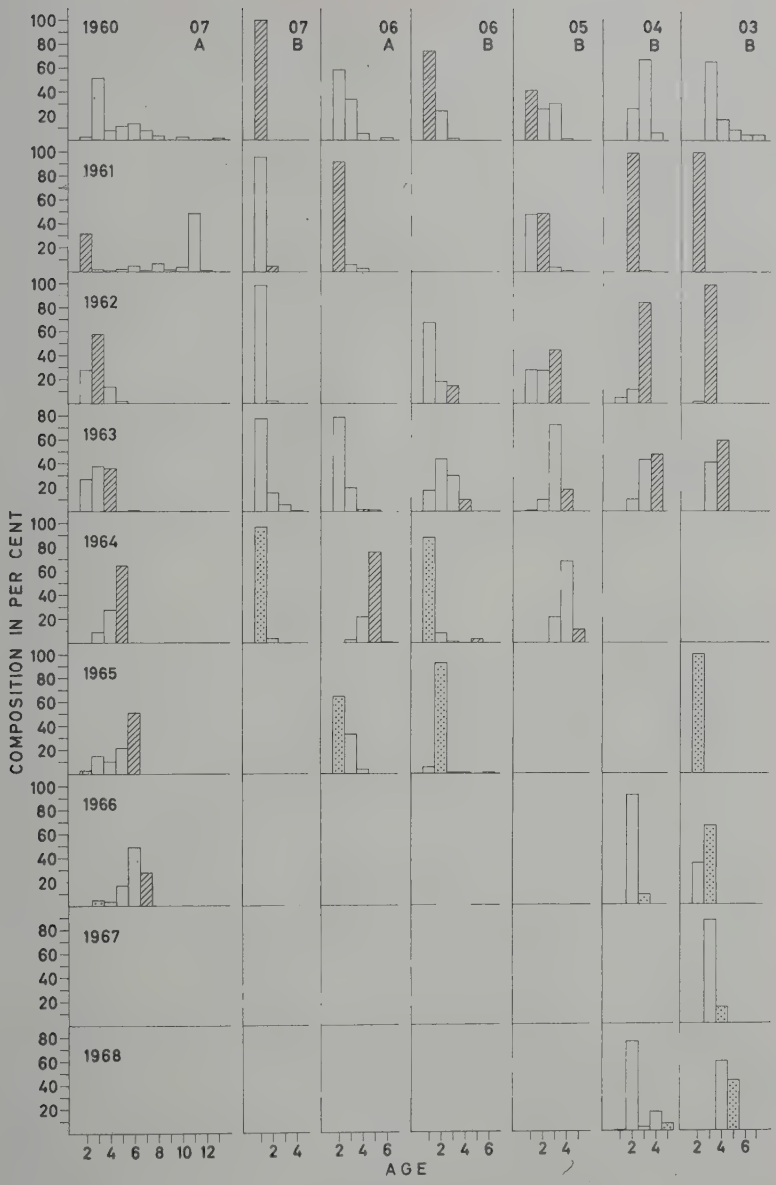

Fig. 30. Age composition (in %) of fat-herring in different areas in 1960–1968, (A) during April–May and (B) during June–December.

Table 5. Yield (in thousands of metric tons) of the 1959–1964 year-classes according to area during the Norwegian fat-herring fishery in 1960–1968.

Year-class	Area					Total
	07	06	05	04	03	
1959	49.558	35.127	65.583	4.108	119.676	274.052
1960	26.652	18.253	97.039	1.571	7.520	151.035
1961	15.660	29.682	25.571	0.368	—	71.281
1962	9.706	8.323	0.273	—	—	18.302
1963*	8.160	22.793	45.123	2.407	189.361	267.844
1964*		0.448	116.890	18.424	268.213	403.975

* Data still incomplete.

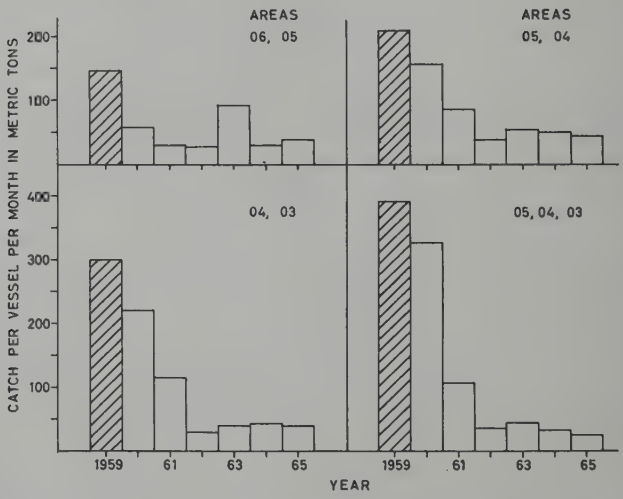

Fig. 31. Average catch of 0-group herring per vessel per month during the autumn fishery (October–December) in 1959–1965.

fleet was more efficient in 1965–1968 than during the previous period when the efficiency was considered to be fairly constant. The more modern sonar equipment introduced during the period 1964–1967 also added to the increase in efficiency of the fleet.

The fat-herring fishery, especially off the Finnmark coast, mainly takes place in the open sea or at the entrances to the large fjords. For this reason and because the availability of fat-herring varies greatly, the abundance estimates for fat-herring are more variable than those for 0-group herring. The abundance estimates for fat-herring, therefore,

have been omitted here. One of the chief problems encountered when dealing with effort statistics from purse seine catches concerns the integration of searching time in the unit of fishing effort. Information concerning the time spent on the fishing grounds or number of shots with and without catch is not available. However, the average catch per vessel operating is likely to give a reasonably reliable indication of the abundance of herring in the different districts.

The average catch of 0-group herring per vessel per month during the autumn fishery from October to December in the different areas is illustrated in Fig. 31. The abundance estimates for areas 05, 04 and 03 combined are higher than those for areas 04 and 03, and 05 and 04 in 1959 and 1960. The reason for the average catch per vessel being higher for areas 05, 04 and 03 combined is due to the larger and more efficient vessels operating in all the three areas. Those operating in areas 04 and 03, 05 and 04 or 06 and 05 are smaller vessels, and the abundance indices for these areas are comparable. The catches per vessel were highest in 1959 followed by 1960 and 1961. In 1962 and 1965 the catches per vessel were lowest in most of the areas.

ESTIMATES FROM TAG RETURNS

Abundance estimates from tag returns are mainly based on taggings of 0-group herring in the Ullsfjord region. For tagging experiments at other localities (Table II) the number of recaptures is too low to permit abundance estimates. Only tags recovered in plants which were equipped with tested magnets have been dealt with quantitatively, and experiments giving less than ten recaptures are excluded in Table 6. The frequencies of returns from 0-group taggings in the fjords were relatively low in 1959–1960, 1960–1961, 1961–1962 and 1963–1964, indicating high abundances of the 1959, 1960, 1963 and 1961 year-classes compared with those of 1962 and 1964. In the autumn of 1965 no 0-group herring were tagged.

Herring catches from different fishing localities were sometimes mixed at the reduction plants before the processing started, and therefore the location of some recaptures could not be determined with certainty. In spite of this limitation the present material indicates that almost all returns during the first months after release were derived from the fjord complex where the tagging took place. This feature was clearest for tagging experiments carried out inside the entrances to the fjords and confirms the findings from acoustic surveys that 0-group herring entering the fjords in autumn stay there the following winter.

A summary of the estimates of year-class strengths at the 0-group stage obtained by the three different methods applied is given in Table 7.

Table 6. Recaptures from taggings of 0-group herring (1959–1964 year-classes) three to seven mon after release and catches of the same year-classes processed at reduction plants. The catches are fr the region of recapture.

Date of tagging		Region of recapture	No. of effectively tagged herring	Effective quantity processed (in tons)	Time from tagging to capture (in months)	No. of recaptures	Percentag recapture per 100 to (inverse value in brackets
1959	2.10	Vesterålen	853	1283	4	10	0.09 (10.
	8.10	Hamarfj.–Ullsfj.–Lyngenfj.	1706	12167	5	237	0.11 (8.
	19.10	Varangerfj.	512	11370	7	63	0.11 (9.
1960	3.10	Hamarfj.–Ullsfj.–Lyngenfj.	1706	30534	6	253	0.05 (20.
	21.10	Varangerfj.	853	10812	6	156	0.17 (5.
1961	28.9	Hamarfj.–Ullsfj.–Lyngenfj.	1706	4970	3	187	0.22 (4.
1962	21.9	Hadselfj.–Vesterålen	1109	45	3	52	10.42 (0.
	27.9	Malangen	512	196	3	58	5.78 (0.
	28.9	Hamarfj.–Ullsfj.–Lyngenfj.	1024	1737	3	203	1.14 (0.
1963	27.9	Hamarfj.–Ullsfj.–Lyngenfj.	1706	2795	4	51	0.11 (9.
1964	29.9	Hamarfj.–Ullsfj.–Lyngenfj.	1706	212	3	128	3.54 (0.

Table 7. Summary showing the results of the abundance estimates of 0-group herring for the 1959–1965 year-classes.

Year-class	Echo abundance index $\times 10^{-3}$		Catch per vessel (in tons) in areas 05, 04, 03 combined	Mean inverse value of percentage recaptures per 100 tons
	Total	Inshore		
1959	325.8	10.4	391.6	9.65
1960	147.4	7.0	325.9	13.25
1961	37.5	6.0	105.0	4.53
1962	14.8	2.5	35.4	0.38
1963	53.6	5.0	44.8	9.35
1964	75.0	3.6	33.6	0.28
1965	9.1	0.7	25.5	—

The results are only comparable for the inshore part of the 0-group population. The inshore abundance estimates obtained from acoustic surveys and those obtained from catch per vessel show the same ranking of the respective year-classes except for those of 1962 and 1964. However,

the discrepancy in the values of the abundance estimates is pronounced for some of the year-classes, especially those of 1962, 1963 and 1964. Because taggings were made in few localities, the abundance estimates obtained from these experiments do not give representative values for year-class strength of the inshore 0-group population.

The estimates of the total 0-group stock obtained from the acoustic surveys indicate that the 1959 year-class was about twice as abundant as the 1960 year-class and this again about twice as abundant as that of 1964. The difference between the 1961 and 1963 year-classes probably was small although the latter year-class was somewhat more abundant. The 1962 and 1965 year-classes definitely were the poorest ones.

MORTALITY

Mortality estimates of herring during the late 0-group and early I-group stages in some Norwegian fjords can be obtained from data on catch per unit of effort and from taggings. The total instantaneous mortality coefficient ($Z = F+M$) for the 1959 and 1960 year-classes was estimated according to the equation of Beverton and Holt (1957)

$$N_t = N_0 e^{-(F+M)t} \qquad (1)$$

where N_0 is the number of fish at the time t_0 and N_t the number of fish at the time t. F and M are the instantaneous fishing and natural mortality coefficients, respectively.

The catch per unit of effort is taken to be proportional to N_0 at the time t_0 and N_t at the time t. During the migration into the fjords the herring are found in many small shoals, and the availability usually is lower than in the wintering period. Because of this the catch per vessel was relatively low in October, and November had to be chosen as the commencement of the fishing season in 1959 and December in 1960. By plotting the logarithms of monthly catches per vessel for November to April in 1959–1960 and for December to April in 1960–1961 and calculating the regression lines to the points, the monthly apparent total mortality ($Z = F+X$) could be estimated (Fig. 32) where F is the monthly fishing mortality and X is a combination of natural mortality and the effect of emigration.

The estimates are given in Table 8, and the basic material used for estimating the catch per vessel is given in Table VII. The values for Z is considerably greater than those obtained for adult herring in the late 1950s and in the 1960s (Dragesund and Jakobsson 1963, Anon. 1969). The monthly instantaneous mortality coefficients are of the same magni-

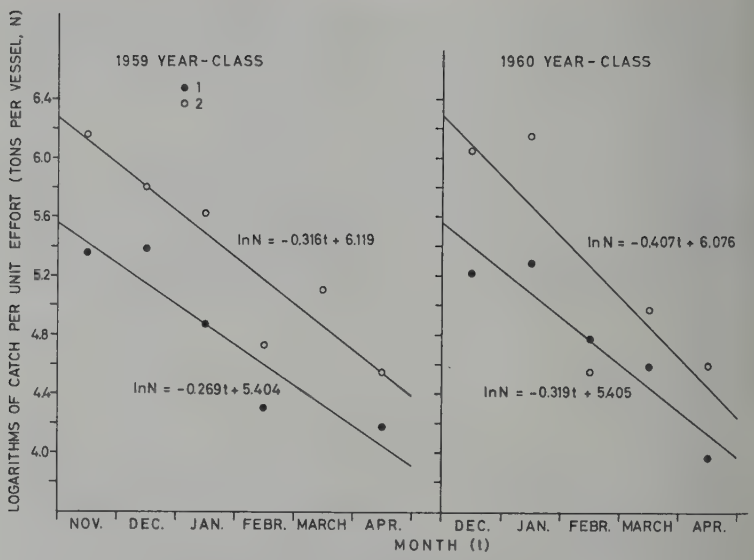

Fig. 32. Calculated regression lines fitted to months and logarithms of catch per vessel, (1) areas 05 and 04, (2) areas 05, 04 and 03.

tude as those of the annual instantaneous mortality coefficients of adult herring.

The exploitation rate (E) defined as

$$E = \frac{F}{F + M} \tag{2}$$

can also be estimated approximately from tag returns by the expression

$$E = \frac{n_r}{N_0 - N_t} = \frac{F}{F + X} \tag{3}$$

where n_r is the estimated number of tagged herring recaptured during the period from t_0 to t, N_0 the number of effectively tagged herring present at the time t_0 and

$$N_t = N_0 e^{-Z(t - t_0)} \tag{4}$$

the number of tagged herring present at the time t. The Z values (F+X) obtained for areas 05, 04 and 03 (Table 8) were used to calculate N_t, and the estimated values for E and Z were used to solve equation (3) for F. The values for N_0, N_t and n_r are listed in Table 9. The estimates

Table 8. Estimates of monthly instantaneous total mortality coefficient (Z) during the late 0-group and early I-group stages covering the period from November to the following April.

Year-class	Area	Z
1959	05 and 04	0.28
	05, 04 and 03	0.32
1960	05 and 04	0.32
	05, 04 and 03	0.41

Table 9. Estimates of number of effectively tagged 0-group herring present (N_0) at the time t_0, number of tagged herring present (N_t) at the time t and number of herring recaptured (n_r) during the period from t_0 to t.

Year-class	Vesterålen			Ullsfjord-Lyngenfjord			Varangerfjord		
	N_0	N_t	n_r	N_0	N_t	n_r	N_0	N_t	n_r
1959	853	237	37	1706	344	382	512	55	84
1960	—	—	—	1706	146	312	853	73	216

Table 10. Estimates of the exploitation rate (E) during the late 0-group and early I-group stages and the monthly instantaneous mortality coefficients F and X, covering the period from November to the following April.

Year-class	Region	E	F	X
1959	Vesterålen	0.060	0.019	0.301
	Hamarfjord–Ullsfjord–Lyngenfjord	0.280	0.090	0.230
	Varangerfjord	0.184	0.059	0.261
1960	Hamarfjord–Ullsfjord–Lyngenfjord	0.200	0.082	0.328
	Varangerfjord	0.277	0.114	0.296

of E, F and X for herring during the late 0-group and early I-group stages from November to April in some of the fjords of northern Norway are given in Table 10.

Another approach for estimating the fishing mortality during the 0- and I-group stages can be obtained from the ratio between catch and stock size of herring wintering in the Ullsfjord region. The stock size was estimated from tag returns by a modification of the Petersen method (Aasen *et al.* 1961, Dragesund and Haraldsvik 1968). The number of tags returned each month during the period from November to April at factories equipped with tested magnets were plotted against the effective quantity processed at the same factories in that month (Fig. 33), and the regression lines were calculated. The stock size was estimated by multi-

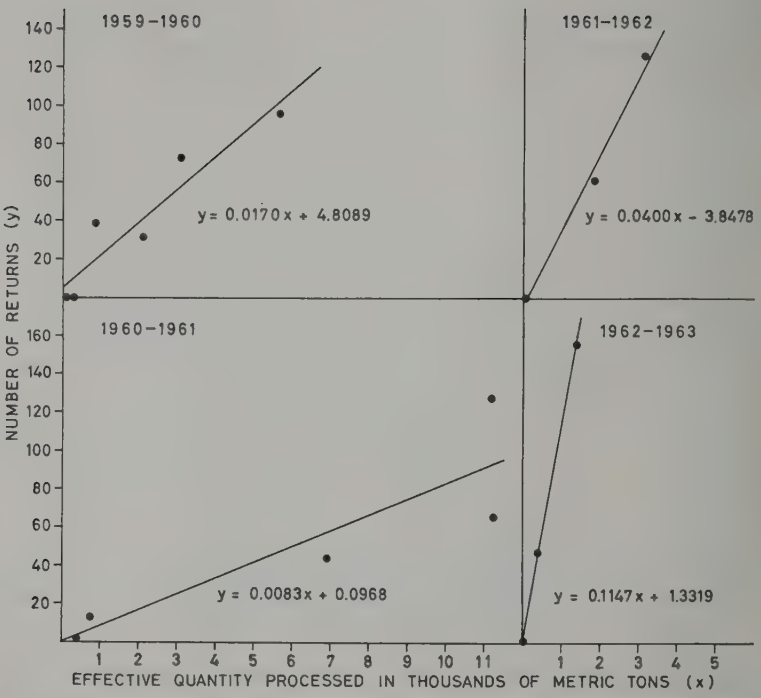

Fig. 33. Calculated regression lines fitted to the monthly catch of 0- and I-group herring processed at factories equipped with magnets and the monthly number of returns.

plying the number of effectively tagged herring present at the beginning of the period by the ratio of the effective quantity processed and the number of returns. This ratio was obtained from Fig. 33.

F was estimated according to the equation of Beverton and Holt (1957)

$$\frac{C}{S} = \frac{F}{Z}(1 - e^{-Zt}) \qquad (5)$$

where C is the catch of herring in numbers and S the stock size in numbers. The Z values for areas 05, 04 and 03 given in Table 8 for the 1959 and 1960 year-classes were used to solve equation (5) for F. To estimate F for the year-classes of 1961 and 1962 the mean of the Z values was used. The results are listed in Table 11.

Although the values for F listed in Tables 10 and 11 are slightly different, they are considerably higher than those obtained from tagging

Table 11. Catch (C), estimated stock size (S) of 0- and I-group herring and estimated monthly instantaneous mortality coefficient (F) during the late 0-group and early I-group stages in the Ullsfjord region for the 1959–1962 year-classes.

Year-class	C		S		F
	Tons	No.	Tons	No.	
1959	19500	279×10^7	91700	1310×10^7	0.085
1960	37600	537×10^7	204700	2924×10^7	0.082
1961	6400	91×10^7	41300	590×10^7	0.085
1962	2900	41×10^7	8800	126×10^7	0.181

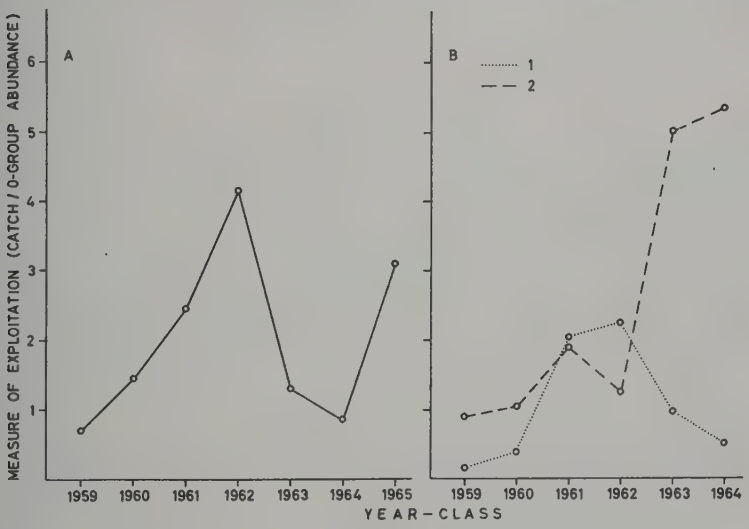

Fig. 34. Measure of exploitation, (A) during the late 0-group and early I-group stages indicated by the ratio of catch in tons/0-group echo abundance for the year-classes 1959–1965 and (B) at later stages for the year-classes 1959–1964, (1) as catch in tons of I- and II-group herring/total 0-group echo abundance and (2) as catch of fat-herring in tons/total 0-group echo abundance.

experiments during the adult stage (Dragesund and Jakobsson 1963, Anon. 1969). The monthly instantaneous fishing mortality coefficients during the late 0-group and early I-group stages are somewhat lower than those of the annual instantaneous mortality coefficients of the adult herring. However, the natural mortality was high for 0- and I-group herring, and accordingly the exploitation rate was lower than for the adult herring in the mid-1960s (Anon. 1969).

Another measure of the exploitation is obtained by taking the ratio between the total catch at different stages of the year-classes 1959–1965

and the total echo abundance index (Fig. 34). It is clearly demonstrated that poor year-classes were more heavily exploited than the rich ones during the late 0-group and early I-group stages (Fig. 34A). Also during the late I-group and early II-group stages the poor year-classes were more heavily fished than the richer ones (Fig. 34B).

The yield of the fat-herring fishery increased considerably from 1965 to 1968. This resulted in an increase of the exploitation of the 1963 and 1964 year-classes by five to six times compared with that of the 1959 and 1960 year-classes. The high exploitation of the 1963 and 1964 year-classes, which appeared to be fairly abundant during the 0-group stage, has most likely resulted in a considerable reduction of these year-classes before they entered the adult stock.

DISCUSSION

DISTRIBUTION OF 0-GROUP HERRING IN RELATION TO SPAWNING GROUNDS OF THE PARENT STOCK

During 1959–1965 the main spawning centre was located off Møre, i.e. on the shelf between Stad and Grip (Dragesund 1970). In 1959–1961 the majority of the ripe herring tended to concentrate farther south than in 1962–1965, when the centre of the spawning was located between Ona and Grip. In the southernmost region (area 08) spawning was negligible except in 1959, when spawning was observed as far south as Bokn. The second important spawning district was located off Halten–Sklinna. Within this region the location of spawning did not change. Except in 1960 (Yudanov 1962) mass spawning at Lofoten was not recorded during 1959–1962, whereas herring spawned regularly in that area in 1963–1965. During 1959–1965 Norwegian herring also spawned on the Faroe plateau (Yudanov 1962, 1964, 1966).

The origin of 0-group herring recorded off northern Norway is difficult to determine. The drift pattern of the larvae from the Faroe spawning grounds is not known, but the international 0-group fish surveys carried out in the Barents Sea and in the northeastern part of the Norwegian Sea in 1966 and 1967 (Anon. 1966, 1967) suggested that the majority of the 0-group fish recorded in the Barents Sea were derived from spawning grounds along the Norwegian coast. Also, the larval survey in 1959 (Wiborg 1959) showed that herring larvae were scarce off the continental shelf in the eastern part of the Norwegian Sea. It is concluded, therefore, that the major part of the herring observed along the coast of northern Norway and in the Barents Sea were hatched off the Norwegian coast between Stad and Grip, off Halten–Sklinna and in 1963–1965 also at the Lofoten spawning grounds.

It also may be concluded that larvae hatched off Møre–Trøndelag drifted far into the Barents Sea. This was indicated by the 0-group distribution in 1959 when no major spawning took place in the Lofoten region. Moreover, in 1959–1961 the 0-group herring were more abundant off Troms and Finnmark (areas 04 and 03) than farther south in areas 06 and 05 (Fig. 31), confirming the hypothesis of a long northward transport of larvae from the spawning grounds off Møre (Dragesund 1970). This indicates that the northward extension of concentrations of 0-group herring does not depend only on the location of spawning, but also on the conditions for transport of larvae from the spawning grounds.

GROWTH AND MIGRATION IN RELATION TO MECHANISM OF RECRUITMENT

The 0-group herring within areas 05, 04 and 03 had fairly uniform lengths. This was to be expected since larvae hatched on the spawning grounds off Møre–Trøndelag are transported northwards in the same water masses and live under rather similar environmental conditions during their first five–six months of life. However, larvae which accumulate at the entrances to the fjords in areas 07 and 06 (off Møre–Trøndelag and the southern part of Nordland) and later enter the fjords in these areas, will live in warmer water and will have a faster growth than those transported farther north.

Herring located off eastern Finnmark were found to have a markedly slower growth during the adolescent phase than those found farther west and south along the coast (Figs. 22 and 23). Herring of the 1959 year-class which stayed in the southern part of the coastal waters of northern Norway (areas 06 and 05) during the 0-group stage, migrated northwards during the second and third years of life, i.e. in 1960 and 1961, and joined the fastest growing herring farther north in an accumulation area off Torsvåg (Figs. 19, 23A and B). These herring started their westward migration into the Norwegian Sea some time during late 1961 or early 1962 and showed up on the feeding grounds off Iceland as early as in the summer of 1962. Herring with slightly smaller annual length increments (1959 year-class) remained in the accumulation area off Torsvåg during the summer and autumn of 1962.

Off Finnmark, slowly growing herring of the 1959 year-class reached an age of three–four years before they disappeared from the fat-herring catches and migrated westward to the accumulation area off Torsvåg from where they later joined the spawning stock. A similar migration pattern was found for the 1960 and 1961 year-classes. Thus, the higher growth rate of herring in the southern part of the coast of northern Norway led to an earlier migration to and from the accumulation area off Torsvåg

than for herring spending their nursery period farther north and east in coastal and offshore waters off northern Norway. Accordingly, fat-herring in areas 06 and 05 were younger than those off Finnmark (area 03), and in the catches south of Vesterålen fat-herring older than three years were scarce, except during the "forfangstsild" season in April–May.

The 1963 and 1964 year-classes showed a different migration pattern compared with those of 1959–1961. During the entire fat-herring stage, i.e. up to an age of four–five years, the 1963 and 1964 year-classes were mainly recorded off eastern Finnmark. Migrations over short distances were observed back and forth between the eastern part of the Finnmark coast and the Murman coast, and in contrast to the 1959–1961 year-classes those of 1963 and 1964 did not concentrate in any detectable shoals off western Finnmark or off Troms during the second to fourth years of life. Their migration from the nursery areas off eastern Finnmark was at least one year delayed compared with the migrations of the 1959–1961 year-classes.

Variations in the occurrence of fat-herring in coastal waters off northern Norway have been discussed by Lea (1929), and variations off the Murman coast by Glebov (1938). According to Lea the large fat-herring (oceanic herring) occur in offshore waters where the herring adopt an oceanic mode of life. Lea concluded that large yields of fat-herring in the fjords were caused by an immigration of oceanic herring. Such immigrations were sporadic and might occur when the oceanic herring were driven towards the coast by unknown causes. Glebov distinguished between two types of immigrations to the fjords, one in May–July consisting mainly of I- and II-group herring, and the other consisting of mainly III- and IV-group herring approaching the coast during the autumn from August onwards. Glebov also found that the immigration was irregular and not always associated with strong year-classes, but was related to hydrographic conditions in coastal and offshore waters. The migration into the fjords was most frequent in years with pronounced horizontal temperature gradients. In the summer the immigration of I- and II-group herring took place when the temperature gradient increased from the open sea into the fjords, whereas in the autumn an immigration of III- and IV-group herring occurred when the temperature gradient decreased from the open sea and into the fjords.

The present investigations showed that the migration of 0-group herring into the fjords was regular and occurred almost at the same time every autumn. It cannot be stated whether the mechanism of the migration from the open sea into the fjords is a response to environmental conditions followed by an orientated active migration or if it is a passive migration resulting from drift (Harden Jones 1968). In Porsangerfjord

the herring moved from water masses of higher to lower temperature, whereas in Ullsfjord this feature was not so clear. No distinct immigration of fat-herring (oceanic herring) to the fjords was recorded. In the years when great concentrations accumulated off northern Norway, mainly in 1961–1963, the fat-herring did not enter the fjords on their migrations from the nursery areas into the Norwegian Sea. With the material at hand no further interpretation can be given of the sporadic immigrations of fat-herring to the fjords of northern Norway. However, in years when the fat-herring stock is large, numerous shoals often occur close to the coast, and it is likely that such shoals may move into the fjords.

When studying the growth of herring, Lea (1929) observed that winter rings of scales from young and adolescent herring caught in northern Norway were more distinct (N-type) than winter rings of herring scales from the coastal area farther south (S-type). Runnstrøm (1936) has given further information on the geographical distribution of the two types. On the Finnmark coast, 100% of the young herring had the northern scale type. In the intermediate region, between Finnmark and the coast of Møre, the N- and S-types were mixed. On the southwest coast about 90% of the young herring had rings of the S-type. From this evidence Runnstrøm concluded that the northern type of winter rings is formed in coastal waters off northern Norway and that the southern type is formed at the southern part of the west coast, thus supporting Lea's theory. According to Lea more diffuse winter rings (oceanic rings) are formed during the adolescent period of transition from immature to mature herring when the herring have moved into the central part of the Norwegian Sea. However, Devold (1963) suggested that the distinct winter rings (N-type) are formed when the young herring live under arctic and subarctic conditions in the Barents Sea. The more diffuse oceanic rings are formed after the westward migration into areas with boreal conditions.

This hypothesis seems to be in agreement with the distribution of 0-group herring of the 1959 and 1961 year-classes and the characteristics of their winter rings. In 1961 relatively few 0-group herring were found in the northern and eastern parts of the Barents Sea, and eventually only a small percentage of the year-class was found to have N-type winter rings. In 1959 the major part of the 0-group stock was distributed in the Barents Sea and on the shelf between Bear Island and West-Spitsbergen. In accordance with this, high percentage of distinct N-type winter rings were found for the 1959 year-class.

According to Østvedt (1958) the relative abundance of N- and S-types in the spawning shoals seemed to be related to year-class strength, high frequencies of N-type herring being correlated with rich year-classes.

The major part of the 1959 year-class had N-type winter rings, whereas the 1961 year-class showed a lower percentage of this growth type both in the adolescent and adult shoals (Table 2). The correlation between rich year-classes and relatively high frequencies of N-type herring may therefore be explained as a result of strong northward transport and high abundance during the larval and postlarval stages.

Ottestad (1934) argued that only part of the fat-herring occurring off northern Norway might later migrate to the spawning grounds off southern Norway (area 08) and the winter herring district off Møre. The majority of fat-herring after becoming mature probably spawned farther north off Lofoten and Vesterålen. According to Lea (1929) the duration of the oceanic stage varies with the individual history of the herring. Some individuals mature after one year, others after two or three years. Each year the maturing herring, which will spawn the following spring, split off from the stock of oceanic herring. In the years 1962–1964 adolescent herring, predominately of the 1959 and 1960 year-classes, were located off Torsvåg during the autumn. Some of these herring matured and migrated to the Lofoten spawning grounds for the first time in 1963 (Devold 1968), whereas others migrated westwards to the feeding areas off Iceland (Jakobsson 1968).

Herring approaching the Lofoten region for spawning in 1963–1966 stayed off northern Norway and in the Barents Sea during the young and adolescent phases. This component, which was separated from the main stock of adult herring both during spawning and on the wintering grounds, did not appear on the Lofoten spawning grounds in the winter of 1967 and 1968 (Devold 1968). In the summer and the autumn of 1966 the two groups had mixed and formed one stock with a spawning migration towards the Møre coast. After this admixture adolescent herring in waters oft Troms and Finnmark and in the Barents Sea therefore will appear on the spawning grounds off Møre somewhat later than those from the nursery areas farther south.

Seliverstova (1968) tried to estimate the abundance of the 1950 year-class which stayed in the Barents Sea during the adolescent phase and to determine the recruitment from the Barents Sea to the adult stock of the 1950 year-class in the Norwegian Sea. A relatively small percentage (1–3%) was found in the adult stock when the year-class was four to five years old, but the percentage increased to about 13–14% at an age of seven and eight years.

No other specific recruitment pattern or mechanism can be discovered from the present data, but it can be concluded that variations in growth may influence the migration pattern and the duration of the adolescent phase. Growth, on the other hand, is determined by the distribution during

the 0-group stage and the 0-group distribution consequently plays an important role in recruitment mechanism. The year by year northward displacement of the main spawning centre, with a corresponding northward displacement of the 0-group population may have been the primary cause for the extended duration of the adolescent phase of the herring of the 1963 and 1964 year-classes.

ABUNDANCE OF 0-GROUP HERRING COMPARED WITH YEAR-CLASS STRENGTH IN THE ADOLESCENT AND ADULT STOCKS

The abundance estimates of 0-group herring show great variations from one year to another. The 1959 and 1960 year-classes were particularly numerous during the 0-group stage. These year-classes also were abundant throughout the adolescent phase and showed up as rich year-classes in the adult stock both on the feeding and spawning grounds (Devold 1968, Dragesund 1970). Similarly, year-classes with low abundance during the 0-group stage, such as that of 1962, appeared to be weak during all the subsequent stages. The 1961, 1963 and 1964 year-classes were considerably more abundant as 0-group herring than those of 1962 and 1965, though clearly less abundant than those of 1959 and 1960.

In Fig. 35 the echo abundance of 0-group herring for the 1959–1962 year-classes is plotted against year-class strength in the adult stock. The values for adult year-class strength (at six years of age) are those obtained from tagging experiments and combined acoustic surveys and underwater photography (Anon. 1969). A very close correlation is found between the two independent estimates of year-class strength, and it is concluded, therefore, that the abundance indices of 0-group herring obtained from the acoustic surveys give a fairly good estimate of year-class strength.

An indication of the relative strengths of the 1959–1965 year-classes in the adolescent and adult stocks can also be obtained from their frequencies in samples collected in different fisheries. These frequencies are compared with estimates of 0-group abundances in Table 12. Samples collected during the different seasons in 1963–1968 clearly demonstrated that the 1959 year-class predominated over the year-class of 1960. In 1964 and 1965 none of the 1962 year-class and only a relatively small part of the 1960 and 1961 year-classes had reached maturity, and consequently the relative strength of the 1959 year-class as indicated by the age distribution was overestimated compared with those of 1960 and 1961. In 1966–1968 the strengths of the 1960 and 1961 year-classes probably were overestimated in relation to the 1959 year-class as mortality had reduced the latter to a greater extent. The age compositions in Table 12 indicate that the relative strength of the 1959 year-class during the adolescent and adult phases was about twice that of 1960 and at least six times that

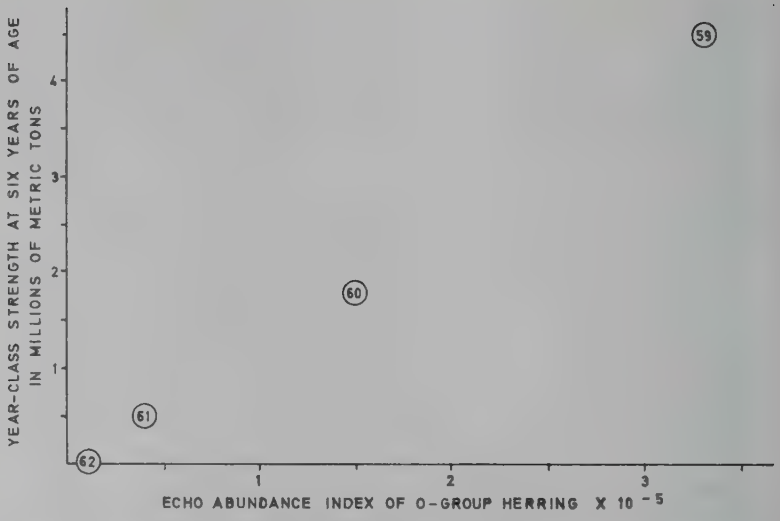

Fig. 35. Relationship between year-class strength at the 0-group stage and at six years of the 1959–1962 year-classes.

of 1961. This conclusion agrees fairly well with the estimates of 0-group abundance obtained from the acoustic surveys (Table 12).

In 1965–1968 none of the 1959–1962 year-classes was found in the fat-herring catches off Finnmark, and it is concluded, therefore, that the majority of these year-classes had migrated from the Barents Sea and the coastal areas off northern Norway. In these years the 1963 and 1964 year-classes dominated in catches off Finnmark (Table 12). Up to 1968 the 1963 and 1964 year-classes had not joined the stock on the spawning grounds in significant numbers. However, in the fat-herring catches (1966–1968) they occurred in about the same ratio as during the 0-group stage. Due to the long adolescent phase the abundance of these herring will be considerably reduced when they reach the adult stage. In addition to the high exploitation of the 1963 and 1964 year-classes, this probably is the primary cause for the absence of these year-classes in the spawning stock in 1968.

EFFECT OF THE NORWEGIAN SMALL- AND FAT-HERRING FISHERIES ON RECRUITMENT TO THE ADULT STOCK

The stock size of adult Norwegian herring increased markedly from 1963 to 1965, primarily because of recruits of the rich year-classes of 1959 and 1960. From 1966 to 1968 a rapid decrease in stock size took place

Year	Month	Region	Year-class							
			1959	1960	1961	1962	1963	1964	1965	Others
1959–1965	Sept.–Oct.	Off northern Norway	*Total 0-group echo abundance* $\times 10^{-3}$							
			325.8	147.4	37.5	14.8	53.6	75.0	9.1	—
			Age composition in %							
1963	Febr.	Ingøy Trench	67.3	28.6	4.1	—				—
	March-April	Off Lofoten	90.9	8.6	—	—				0.5
	June–July	Off eastern Finnmark	7.5	81.3	11.2	—				—
	July–Aug.	Off Iceland	22.9	2.3	0.3	—				74.5
	Oct.–Nov.	Off Torsvåg	43.0	42.1	14.6	—				0.3
1964	Febr.	Off Møre	51.5	4.0	—	—	—			44.5
		Off Lofoten	88.4	10.1	0.6	—	—			0.9
	July–Aug.	Off Iceland	46.8	10.1	4.0	0.1	—			39.0
	Aug.–Sept.	Area 37	70.6	21.2	7.9	—	—			0.3
1965	Febr.–March	Off Møre	62.7	10.7	3.2	—	—	—		23.4
		Off Lofoten	74.1	19.6	5.8	—	—	—		0.5
	July–Aug.	Off Iceland	42.3	12.7	5.8	0.4	1.5	—		37.3
	Aug.	Off Finnmark	—	—	—	—	64.4	35.6		—
1966	Febr.–March	Off Møre	53.4	27.7	10.3	0.1	—	—	—	8.5
		Off Lofoten	51.6	39.1	8.0	0.3	—	—	—	1.0
	July–Aug.	Off Iceland	49.8	18.7	7.9	0.8	2.7	—	—	20.1
	Aug.	Off Finnmark	—	—	—	—	29.6	52.5	17.9	—
1967	Febr.–March	Off Møre	48.8	32.1	13.4	0.4	0.5	—	—	4.8
	June–Aug.	Off Finnmark	—	—	—	—	33.9	66.1	—	—
	July–Aug.	Off Iceland	50.3	31.8	11.6	1.1	1.2	0.1	—	3.9
1968	Febr.–March	Off Møre	46.9	34.2	13.8	1.7	0.7	—	—	2.7
	April–May	Off Finnmark	—	—	-	—	41.9	58.1	—	—
	July–Sept.	Off Iceland	47.2	31.4	13.0	2.1	2.4	0.2	0.1	3.6

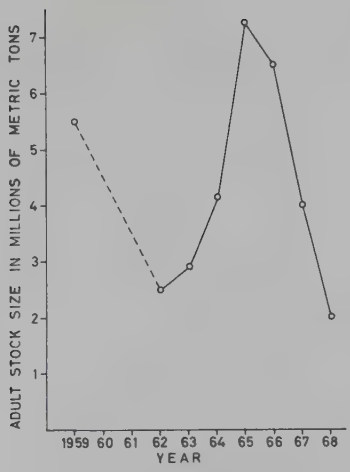

Fig. 36. Stock size of adult Norwegian herring in 1959 –1968 (Anon. 1969).

(Fig. 36). During this period the stock should have been recruited from the 1962–1964 year-classes. Although the exploitation during the late 0-group and early I-group stages was nearly the same for these year-classes as for those of 1959–1961 (Fig. 34), they did not show up in significant numbers in the adult stock. The ratios of the yield of the separate year-classes of 1959–1965 in the small-herring fisheries and the echo abundance of 0-group herring (inshore) show that the exploitation of 0- and I-group herring in the fjords generally has fluctuated in accordance with the abundance of herring (Fig. 37). It is concluded, therefore, that the variations in recruitment to the adult stock during the 1960s cannot be attributed to the fishery on 0- and I-group herring.

Fedorov, Truskanov and Yudanov (1963) pointed out that for adults the ratio between the strengths of weak and strong year-classes on the basis of catches was 1/8–1/14, while the ratio of the same year-classes in the small-herring catches was only 1/2–1/3. They take this to support their claim that the fishery on small-herring was an important factor determining recruitment during the late 1950s and early 1960s. Marti (1959), dealing with year-classes prior to those of 1959–1965, held the opinion that year-classes which were heavily fished as young, gave relatively smaller catches as adults than those which were lightly fished prior to recuitment to the adult stock.

Fig. 38 shows the ratios between year-class strength of the 1959–1963 year-classes at the 0-group stage and at six years. Adult year-class strength for that of 1963 is based on a spawning stock size in 1969 of 1.3 million tons. This stock size was estimated from data in the report of the Atlanto-

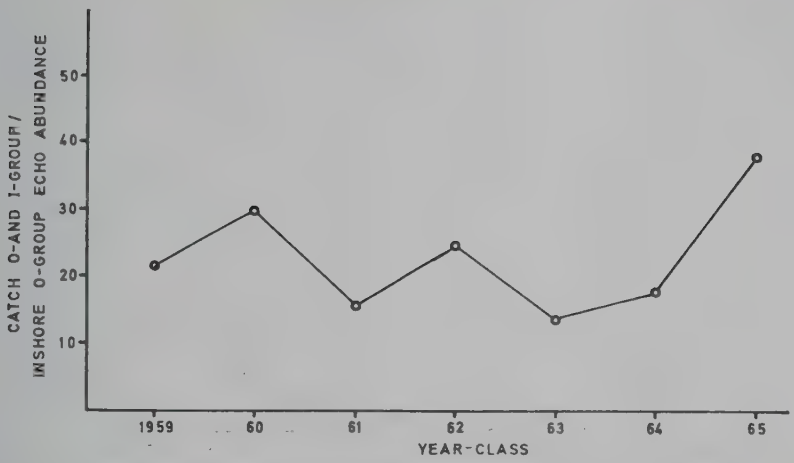

Fig. 37. Ratio between catch (in tons) of 0- and I-group herring in Norwegian fjords and inshore echo abundance of 0-group herring of the 1959–1965 year-classes.

Scandian Herring Working Group (Anon. 1969) applying a total annual mortality coefficient of $Z = 0.44$. For the 1964 and 1965 year-classes no adult abundance indices can be given.

There is no marked difference in the ratios between year-class strengths in the 0-group and the adult stocks of the 1959–1961 year-classes. However, the ratios of the 1962 and especially the 1963 year-classes were relatively higher. This indicates that these year-classes have been more reduced in numbers during the young and adolescent phases than the 1959–1961 year-classes. The exploitation of the 1962 year-class was higher during the 0- and I-group stages than that of 1963 (Fig. 34). The same was the case for the 1961 year-class compared with that of 1963, but the effect of this could not be measured in the adult stock. It is difficult, therefore, to verify whether the relative abundance of poor year-classes decreased markedly compared with the rich ones because of exploitation during the late 0-group and early I-group stages in the Norwegian fjords. However, the high natural mortality rate during these stages and the relatively low percentage of the 0-group stock present in the fjords suggest that the small-herring fishery was not a determining factor for the total mortality of year-classes up to 1965 before they were recruited into the adult stock.

The exploitation of the 1963 and 1964 year-classes during the fat-herring stage was five to six times higher than for the 1959 and 1960 year-classes, and this is assumed to have reduced the number of recruits of the 1963–1964 year-classes markedly. Since the fat-herring are exploited in

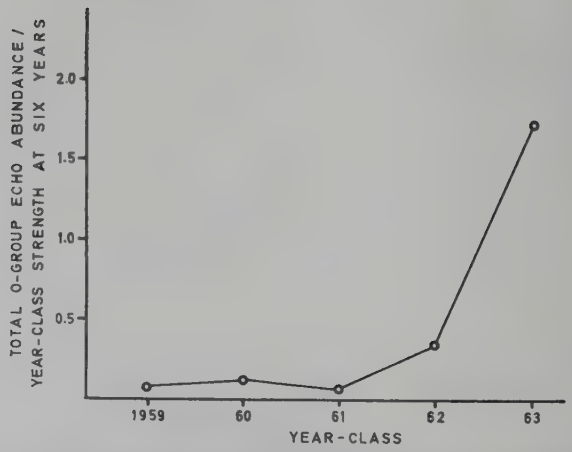

Fig. 38. Ratio between total 0-group echo abundance and year-class strength at six years (in tons) of the 1959–1963 year-classes.

offshore waters and natural mortality is most likely considerably lower than for 0- and I-group herring, the fat-herring fishery may be expected to have a relatively greater effect on recruitment to the adult stock than the small-herring fishery on 0- and I-group herring in the Norwegian fjords. No exact estimate can be made of the impact of the Norwegian small- and fat-herring fisheries on subsequent recruitment to the adult stock for the year-classes of 1959–1965. However, tentative estimates have been made for the strong year-class of 1959 and the weaker year-class of 1963 to study the possible reduction of year-class strength at six years caused by the fishery on young and adolescent herring using alternative values of natural mortalities.

The catches of 0- to III-group herring by month and district are listed in Tables VIII and IX. The catches were converted to numbers and reduced according to the equation

$$N_t = N_0 e^{-Mt} \qquad (6)$$

where N_0 is the number of herring at the time t_0 and N_t at the time t. M is the instantaneous natural mortality coefficient.

Little is known about natural mortality of young and adolescent herring except for the late 0- and early I-group stages (Table 10). Because data on loss of tags are uncertain and the emigration of herring may have affected the estimates, fishing mortality is most likely underestimated. Consequently, the natural mortality may have been overestimated, and

therefore the lowest monthly apparent natural mortality (X = 0.23) was used for the wintering period (October to April) of 0- and I-group herring in the fjords. This value corresponds to an annual M_1 of 2.76 (Table 13).

It may be assumed that natural mortality is considerably reduced after the second growth season when most of the herring have nearly doubled their lengths (Table VI). Swimming speeds increase with the lengths. Blaxter and Dickson (1959) found that captive herring ranging from 1–25 cm swam at speeds (for distances at least ten times their body length) of 3–175 cm/sec. Herring 20–25 cm long could swim at nearly maximum speed for 1100 lengths. It is likely, therefore, that the predator effect will decrease with length and that the natural mortality is inversely related to length. When the herring have moved from the coast and the central parts of the Barents Sea, they have relatively few predators, and in the late adolescent phase the annual natural mortality may be of the same magnitude as in the adult phase, i.e. M = 0.16 (Anon. 1965).

Tentatively, the monthly instantaneous natural mortality coefficient during the late I- and early II-group stages has been graded down to one fourth, one half and three quarters of that in the late 0- and early I-group stages, i.e. to 0.0575, 0.115 and 0.173, respectively, corresponding to annual instantaneous mortality coefficients (M_2) of 0.69, 1.38 and 2.07 (Table 13). These three alternative M_2 values were used to calculate the reduction from May in the I-group stage to April in the II-group stage. For the period from May in the II-group stage to 1 January in the VI-group stage the annual instantaneous mortality coefficients (M_3, M_4, M_5, M_6) are assumed to be equal, and two different values (0.16 and 0.24) were used. The estimated number of herring at the VI-group stage (by 1 January) was converted to tons by applying average weights of 217 and 232 g for herring from nursery areas in Troms–Finnmark and Møre–Trøndelag–Nordland, respectively (W_1, Table 13).

In order to evaluate the loss due to fishing on 0- to III-group herring, catches at subsequent stages (up to age six by 1 January) were estimated. The catches in numbers for the 1959 and 1963 year-classes in the adult fisheries are taken from the report of the Atlanto-Scandian Herring Working Group (Anon. 1969). The yield from the pre-recruit fisheries (fat-herring and "forfangstsild") in Norwegian coastal waters after age of three years (by April) are given in Tables X and XI. The total catches were reduced according to the alternative M_3, M_4, M_5, M_6 values listed in Table 13 and converted to tons (W_2). The loss due to catches of young and adolescent herring can be found from the expression

$$\frac{W_1}{W_1+W_2+S_6}\,100 \qquad (7)$$

Table 13. Estimates of percentage loss to year-class strength at six years due to the catches of young and adolescent herring of the 1959 and 1963 year-classes. Catches and year-class strengths are given in thousands of metric tons.

Year-class	Alternative values of annual natural mortality			Loss due to catches of		Year-class strength at six years S_6	Percentage loss $\frac{W_1 \cdot 100}{W_1+W_2+S_6}$	Loss due to catches of 0- to I-group w_1	Percentage loss $\frac{w_1 \cdot 100}{W_1+W_2+S_6}$	Loss due to catches of I- to II-group w_2	Percentage loss $\frac{w_2 \cdot 100}{W_1+W_2+S_6}$	Loss due to catches of II- to III-group w_3	Percentage loss $\frac{w_3 \cdot 100}{W_1+W_2+S_6}$
	M_1	M_2	$M_3 \ldots M_6$	0- to III-group W_1	III- to V-group W_2								
1959	2.76	0.69	0.16	1345	809	4501	20.2	682	10.2	402	6.0	261	3.9
	2.76	1.38	0.16	873	809	4501	14.1	342	5.5	270	4.4	261	4.2
	2.76	2.07	0.16	622	809	4501	10.5	172	2.9	189	3.2	261	4.4
	2.76	0.69	0.24	1006	728	4501	16.1	508	8.1	300	4.8	198	3.2
	2.76	1.38	0.24	654	728	4501	11.1	255	4.3	201	3.4	198	3.4
	2.76	2.07	0.24	467	728	4501	8.2	128	2.2	141	2.5	198	3.5
1963	2.76	0.69	0.16	529	537	31	48.2	111	10.1	101	9.2	317	28.9
	2.76	1.38	0.16	442	537	31	43.8	55	5.4	70	6.9	317	31.4
	2.76	2.07	0.16	394	537	31	41.0	27	2.8	50	5.2	317	33.0
	2.76	0.69	0.24	397	473	31	44.1	82	9.1	75	8.3	240	26.6
	2.76	1.38	0.24	333	473	31	39.8	41	4.9	52	6.2	240	28.7
	2.76	2.07	0.24	298	473	31	37.2	21	2.6	37	4.6	240	29.9

where S_6 is the estimated size in tons of the year-class at six years assuming full recruitment at this age.

The estimates show that the catches of 0- to III-group herring may have reduced the 1959 year-class at six years by 8.2–20.2% and the 1963 year-class by 37.2–48.2%. This again shows that the exploitation of the 1963 year-class during the young and adolescent phases was considerably higher than for the 1959 year-class, and taking into account the subsequent catches (up to age six) nearly all the herring of the 1963 year-class were caught before recruitment into the adult stock.

The effect of fishing on the different age groups can be analysed by splitting the loss (W_1) on 0- and I-group (w_1), I- and II-group (w_2) and II- and III-group (w_3) herring (Table 13). The loss due to catches of 0- and I-group herring may have reduced the 1959 and 1963 year-classes by 2.2–10.2%. Taking into account that the fjord population of the 1959 year-class was only about 3% of the 0-group population and about 10% of the 1963 year-class, it may be assumed that the higher estimates in Table 13 represent an overestimate of the loss due to fishing on 0- and I-group herring.

Further calculations have been made to estimate the yields which might have been obtained from the loss due to the catches of 0- to III-group herring if exploitation had started by 1 January at six years of age and continued throughout the lifespan up to an age of eighteen years. The number of fish by 1 January at six years of age is denoted by N_6. When estimating N_6 the two highest and lowest values of M_2 were excluded. The number by 1 January the following year (N_7) can be estimated from the expression

$$N_7 = N_6 e^{-Z} \qquad (8)$$

where $Z=(F+M)$ is the total annual instantaneous mortality coefficient.

The catch in numbers from age six to seven is given by

$$C_6 = \frac{F}{F+M}(N_6 - N_7) = \frac{F}{F+M} N_6 (1 - e^{-(F+M)}) \qquad (9)$$

and from age seven to eight by

$$C_7 = \frac{F}{F+M} N_7 (1 - e^{-(F+M)})$$

etc. to

$$C_{18} = \frac{F}{F+M} N_{18} (1 - e^{-(F+M)})$$

It has been assumed that

$$E = \frac{F}{F + M} \text{ and } Z = (F+M)$$

do not change for age groups from six to eighteen years. Average values of exploitation rate (E = 0.64) and total annual instantaneous mortality coefficient (Z = 0.44) for the 1959–1961 year-classes, which were obtained from the report of the Atlanto-Scandian Herring Working Group (Anon. 1969), have therefore been used in the estimates (Table XII). The annual catches in numbers have been converted to tons and compared with the actual catches of 0- to III-group herring (Table 14). The estimates show that about the same yield in weight would have been obtained already at the end of the third year of exploitation (starting the fishery at six years of age), and the total yield over the life-span (from six to eighteen years) would have been considerably higher.

The tentative estimates are based on too few exact observations on natural mortality during the young and adolescent phases, and unknown factors may change the results completely. Nevertheless, they indicate that the fishery for young and adolescent herring may effect the subsequent recruitment to the adult stock considerably. The high exploitation of the 1963 year-class during the fat-herring stage thus probably resulted in a marked reduction of this year-class before it entered the adult stock.

Table 14. Catches of 0- to III-group herring of the 1959 and 1963 year-classes, and estimates of yield which might have been obtained by refraining from these catches and by starting the exploitation at six years of age. The catches are given in thousands of metric tons. See Table XII for further information.

Year-class	Category	Catch	Estimated yield		
			Year	Alternative 1	Alternative 2
1959	0- and I-group	176	1965	203	152
	I- and II-group	109	1966	141	105
	II- and III-group	93	1967	110	82
	0- to III-group	378	1965–1967	454	339
			1968–1977	215	162
			1965–1977	669	501
1963	0- and I-group	45	1969	102	78
	I- and II-group	36	1970	71	54
	II- and III-group	114	1971	55	42
	0- to III-group	195	1969–1971	228	174
			1972–1981	108	83
			1969–1981	336	257

Both the small- and fat-herring fisheries fluctuate according to variations in year-class strength, but other biological factors, such as distribution, growth and migration also influence the yield of these fisheries. The decline in the catches of Norwegian winter herring in the late 1950s and early 1960s, the increase in the mid-1960s and the decrease in 1967–1968 were primarily associated with variations in year-class strength and not with the Norwegian small-herring fishery in the fjords. However, an extension of the 0-group herring fishery to the open sea, and a high exploitation rate of fat-herring will result in an appreciable reduction in the subsequent abundance in the adult stock. Environmental factors presumably play a major role in determining the reproductive success of the stock (Dragesund 1970). However, with the spawning stock size at a relatively low level an intensified fishery may endanger the prospects for future reproduction of the stock of Norwegian herring. Any increase in the fishing rate should be avoided, and a reduction of the fisheries on young and adolescent herring should be considered to improve the abundance of adult herring.

SUMMARY

1. The distribution of young and adolescent herring in coastal and offshore waters of northern Norway has been investigated for the 1959–1965 year-classes by combined acoustic surveys and fishing experiments.

2. In the autumn (August–October) 0-group herring occur pelagically in the upper 50 m of water together with the 0-group of several other species, such as cod, haddock, redfish, capelin and others. This complicates the charting and identification of the sound scatterers, but detailed studies of the echo recordings and frequent sampling in the scattering layer made it possible to determine the distribution of 0-group herring.

3. In 1959, 1960, 1964 and to some extent in 1963 and 1965, 0-group herring had an oceanic distribution, and only a minor part of the 0-group population entered the fjords of northern Norway. In 1961 and 1962 the distribution was more restricted to the coastal areas, and a greater proportion of the total 0-group population was present in the fjords. Herring entering the fjords at the 0-group stage in the autumn emigrate during the I-group stage from March to May.

4. Herring in the northern and eastern Barents Sea had slower growth rates and consequently a longer phase of migration to the spawning areas than did those distributed farther south and west. Herring from nursery grounds in the Barents Sea, therefore, are considerably more reduced in numbers before they reach the spawning grounds off Møre than those

which have spent their 0-group stage in the southern nursery areas in Norwegian coastal waters. The growth rate, therefore, may influence the migration pattern and the duration of the adolescent phase. Growth on the other hand is determined by the distribution during the 0-group stage, and the 0-group distribution consequently plays an important role in recruitment mechanism.

5. Abundance estimates of 0-group herring were obtained from three independent sources, i.e. acoustic surveys, catch and effort statistics and tagging experiments. The 1959 year-class, but also that of 1960, were numerous during the 0-group stage and remained abundant throughout the adolescent phase and in the adult stock. Year-classes of low abundance at the 0-group stage, such as the 1962 year-class, remained weak throughout the subsequent stages. The 1963 year-class, which was fairly abundant as 0-group, did not show up in significant numbers in the adult stock in 1968 and 1969. The 1964 and 1965 year-classes have not been studied in their adult phase because they had not attained maturity when the material was compiled. The year-classes of 1963 and 1964 showed about the same relative strengths during the adolescent phase as at the 0-group stage.

6. Mortality estimates obtained from catch and effort data and tagging experiments indicate that the fishing mortality of 0- and I-group herring in Norwegian fjords was relatively high, but because natural mortality was much higher, the exploitation rate was relatively low. Taking into account that the fjord population is only part of the total 0-group population, it is concluded that the fishing mortality generated by the 0- and I-group fishery in Norwegian fjords was too small to be the primary cause of the failure of recruitment to the adult stock.

7. A considerable increase in the exploitation of fat-herring, i.e. I- to IV-group herring took place from 1965 to 1968. The increase in exploitation during the adolescent phase of the 1963 and 1964 year-classes compared with those of the 1959–1961, and a long duration of the migration of the former year-classes from the nursery areas to the spawning grounds may explain why the year-classes of 1963 and 1964 tended to be relatively weak in the adult stock.

8. With the relatively low level of the spawning stock size an intensified fishery on the Norwegian herring should be avoided. An extension of the small- and fat-herring fisheries into the open sea may result in an appreciable reduction in the subsequent abundance in the adult stock, and a reduction of the fishery on young and adolescent herring should be considered to improve the abundance of adult herring.

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Table I. Records of fishing experiments with pelagic trawl (PT), purse seine (PS), bottom trawl (BT) and Isaacs–Kidd ten foot mid water trawl (IKMT) for identification of echo traces during the surveys in 1959–1965.

Area	Date	Gear	No. of hauls, shots or samples	No. of fish per nautical mile towed or per purse seine shot				
				Year-class of herring				Other species
	1959			1959	1958	1957	1956	
06	27.9	PT	1	611	—	—	—	Not identified
05	30.9–2.10	PS	3	18438	—	—	—	Not identified
	6.10	PT	1	213	—	—	—	Not identified
04	9.10	PT	1	8520	—	—	—	Not identified
	8.10	PS	1	685000	—	—	—	Not identified
03	18–20.10	PS	3	35032	—	—	—	Not identified
	22.10	PS	1	A few hl				
	20.10	PS	1	Ca. 100 hl, mainly of 1957, 1958 year-classes				
02 and 10	15–16.10	Stomach content	2	8	—	—	—	Not identified
13	8.10	Stomach content	1	15	—	—	—	Not identified
15	12.10	Stomach content	1	24	—	—	—	Not identified
20	3.9	Stomach content	1	10	—	—	—	Not identified
	3.9–20.10	Stomach content	2	Many/some	—	—	—	Not identified
	20.10	BT with cover	1	200	—	—	—	Not identified
21	9–16.10	BT with cover	4	8	—	—	—	Not identified
	9.10	Stomach content	3	Some	—	—	—	Not identified
25	10.10	Stomach content	1	Some	—	—	—	Not identified
	12.10	BT with cover	1	1	—	—	—	Not identified
23	10.10	Und. wat. photogr.	1	Identified as 0-gr. herring, 1959 year-class				

Table I (*continued*)

1960				1960	1959	1958	1957	
05	28.9–2.10	IKMT	8	45	—	—	—	12
	29.9–2.10	PT	2	15	—	—	—	1
	29.9	PS	1	266	—	—	—	8
04	2–23.10	IKMT	4	4	—	—	—	—
	2–23.10	PT	2	2649	3	—	—	6
	3–24.10	PS	3	298259	80	—	—	—
03	10.10	IKMT	1	7	—	—	—	1
	21–22.10	PT	2	824	A few	—	—	—
	19–21.10	PS	3	1064	2	—	—	17
03 and 10	13.9–11.10	IKMT	4	11	—	—	—	14
02 and 10	13.9–14.10	PS	3	Ca. 1300	46	—	—	54
04 and 12	23.9–8.10	IKMT	4	1	1	—	—	3
12	8.10	PT	1	—	2326	24	24	1
13	15.9–13.10	IKMT	3	2	—	—	—	2
	13.10	PT	1	25	11	—	—	49
15 and 23	16.9–12.10	IKMT	4	7	—	—	—	523
15	12.10	PT	1	13	—	—	—	53
20	21.9–8.10	IKMT	8	139	1	—	—	4
	22.9–5.10	PT	3	371	—	—	—	28
	7.10	PS	1	Ca. 40000	—	—	—	—

Table I (*continued*)

Area	Date	Gear	No. of hauls, shots or samples	No. of fish per nautical mile towed or per purse seine shot				
				Year-class of herring				Other species
	1961			1961	1960	1959	1958	
05	4.9	IKMT	1	2	—	—	—	39
	3–28.9	PT	6	82	—	—	—	5
	6–27.9	PS	2	26540	60	—	—	—
04	23–26.9	PT	7	83	1	—	—	26
	25.9	PS	1	4808	—	—	—	—
03	21–23.9	PT	5	70	1	1	—	13
	20.9	PS	1	7370	1211	519	—	—
03 and 10	17–20.9	PT	5	19	1	1	—	44
03	22.9	PS	2	15	2	25762	—	—
04 and 12	9–12.9	PT	2	4	1	—	—	23
12	11–12.9	PS	2	3	34	1008	—	—
11	23.11	PT	1	—	4	4	—	—
13	1.8–20.11	PT	2	Ca. 80 l mixture of I- and II-group herring 1959–1960 year-classes and 0-group cod and haddock.				
20	9.9	PS	1	3	—	—	—	721
	1962			1962	1961	1960	1959	
05	21–23.9	PT	3	40023	5	—	—	1
	21–27.9	PS	4	577066	25705	803	268	—
04	17.9	PT	2	1630	17	—	—	49
	28–29.9	PS	3	15188	700	2	—	—
03	13.9	IKMT	1	2	—	—	—	—
	13.9	PT	2	22	29	147	107	—
03 and 10	5–7.9	IKMT	2	4	—	—	—	1
	6.9–5.11	PT	7	135	82	253	198	—
04 and 12	12.9–16.11	PT	3	1	1	4	5	5
	18–29.9	PS	2	—	1326	3583	25023	—

Table I (*continued*)

1963				1963	1962	1961	1960	
05	3.10	IKMT	1	1	—	—	—	1
	4.10	PT	1	280	—	—	—	—
	4.10	PS	1	13424	—	—	—	—
04	2.10	IKMT	1	1	—	—	—	35
	30.9–6.10	PT	2	96	—	3	14	—
	27.9–1.10	PS	6	35024	—	865	1575	—
03	30.8–17.9	IKMT	4	11	—	—	—	14
	18–20.9	PT	2	552	—	—	—	2
10	20–21.9	IKMT	2	3	—	—	—	30
	20.9	PT	1	39	—	—	—	2 litres
13	11.9	IKMT	1	18	—	—	—	33
14	4.9	IKMT	1	3	—	—	—	5
20	11.9	IKMT	1	8	—	—	—	11
	24.9	PT	1	126	—	—	—	6
1964				1964	1963	1962	1961	
05	12.8–1.10	PT	2	2362	1	—	—	3
04	10.9	IKMT	1	2	—	—	—	—
	10–28.9	PT	2	10769	—	—	—	1
	29.9	PS	2	16870	—	—	—	1
03	15–21.9	PT	2	204	15	—	—	129
	16–25.9	PS	2	10939	340	—	—	20
10	15.9	IKMT	1	2	—	—	—	65
02 and 10	13–14.9	PT	4	169	1	—	—	—
12	11.9	IKMT	1	2	—	—	—	24

Table I (*continued*)

Area	Date	Gear	No. of hauls, shots or samples	No. of fish per nautical mile towed or per purse seine shot				
				Year-class of herring				Other species
	1964			1964	1963	1962	1961	
04 and 12	10.8–26.9	PT	9	312	1	—	—	—
13	13.9	IKMT	1	5	—	—	—	3
	11–23.9	PT	3	95	—	—	—	—
15	23.9	PT	1	20	—	—	—	404
20	8.9	IKMT	1	4	—	—	—	161
	2–23.9	PT	2	14	—	—	—	222
21	23.7–6.9	PT	5	130	—	—	—	—
37	31.8–1.9	PT	2	—	—	—	—	24
	1965			1965	1964	1963	1962	
05	25–27.8	PT	3	38	—	—	—	—
04	30.8	PT	2	192	—	—	—	4
03	31.8	PT	2	—	1697	2128	—	3
12	9–14.9	PT	2	16	—	—	—	257
21	10–11.9	PT	2	25	—	—	—	862

Table II. Tagging experiments with internal steel tags on young and adolescent herring in coastal and offshore waters of northern Norway in 1959–1964.

Date		Position	Category of herring	No. of herring tagged
1959	1.10	N 67° 50′, E 14° 10′	0-group	600
	2.10	N 68° 40′, E 12° 45′	0-group	1000
	8.10	N 70° 10′, E 19° 30′	0-group	2000
	19.10	N 69° 50′, E 30° 30′	0-group	600
1960	3.10	N 70° 10′, E 19° 30′	0-group	2000
	7.10	N 74° 30′, E 19° 30′	0 group	2000
	14.10	N 70° 20′, E 36° 30′	0-group	1500
	14.10	N 69° 20′, E 37° 20′	I-group	1000
	21.10	N 70° 03′, E 29° 50′	0-group	1000
	23.10	N 70° 50′, E 26° 00′	0-group	300
1961	6. 9	N 69° 20′, E 17° 00′	0-group	1000
	20. 9	N 69° 50′, E 30° 30′	0-group	1000
	20. 9	N 69° 50′, E 30° 30′	I-group	200
	25. 9	N 70° 10′, E 19° 30′	0-group	2000
	27. 9	N 69° 35′, E 17° 25′	0-group	500
	12. 9	N 71° 35′, E 25° 35′	Fat-herring	950
	22. 9	N 71° 35′, E 27° 45′	Fat-herring	500
1962	21. 9	N 68° 30′, E 15° 00′	0-group	1300
	25. 9	N 67° 10′, E 13° 50′	0-group	600
	27. 9	N 69° 18′, E 18° 40′	0-group	600
	28. 9	N 69° 35′, E 19° 40′	0-group	1200
	18. 9	N 71° 40′, E 19° 35′	Fat-herring	1900
	21. 9	N 68° 30′, E 15° 00′	Fat-herring	800
1963	27. 9	N 69° 35′, E 19° 40′	0-group	2000
	4.10	N 68° 30′, E 15° 00′	0-group	1000
	17. 6	N 69° 50′, E 30° 30′	I-group	300
	19. 6	N 70° 15′, E 34° 00′	I-group	900
	5. 6	N 70° 10′, E 32° 30′	Fat-herring	600
	10. 6	N 70° 10′, E 32° 30′	Fat-herring	400
	19. 6	N 70° 15′, E 34° 00′	Fat-herring	100
	25. 6	N 69° 10′, E 16° 30′	Fat-herring	400
	1.10	N 71° 10′, E 20° 00′	Fat-herring	1000
1964	16. 9	N 70° 03′, E 29° 50′	0-group	1000
	25. 9	N 70° 50′, E 26° 00′	0-group	1000
	29. 9	N 69° 35′, E 19° 35′	0-group	2000

Table III. Length distribution (in cm) of 0-group herring of the 19

Year-class	Area	Date	Gear	No.	6.0	6.5	7.0	7.5	8.0	8.5
1959	05	1.10	PS	648						6
		2.10	PS	456						
		16.11	PS	608			18	33	37	54
	04	8.10	PS	685				3	9	33
		19.10	PS	793			8	26	78	130
		19.10	PS	661		3	—	23	52	76
		30.10	PS	613		2	12	18	42	70
		10.11	PS	617	1	—	3	—	5	11
		17.11	PS	764				9	19	87
		20.11	PS	570			1	3	12	45
		20.11	PS	833		1	3	22	59	129
		21.11	PS	712		3	18	38	55	108
		21.11	PS	838				18	55	118
		22.11	PS	577				5	7	52
		23.11	PS	459					2	5
		23.11	PS	789				9	35	106
		23.11	PS	649			4	6	25	64
		23.11	PS	729			26	103	159	150
		24.11	PS	772				4	18	47
		2.12	PS	868			3	19	54	89
		2.12	PS	886			10	26	59	108
		8.12	PS	723			9	15	29	53
		8.12	PS	824			22	51	76	117
	03	18.10	PS	1176				8	318	427
		19.10	PS	1384			24	210	431	277
		20.10	PS	725			19	22	23	43
		22.10	PS	814					12	95
		26.10	PS	774			1	3	16	71
		23.11	PS	531			4	23	52	76
		24.11	PS	583			12	32	65	88
		24.11	PS	836			26	57	104	117
		27.11	PS	885			5	33	157	200
		1.12	PS	880			1	48	151	193
		1.12	PS	956			16	101	180	176

55 year-classes caught with purse seine (PS) and pelagic trawl (PT).

9.0	9.5	10.0	10.5	11.0	11.5	12.0	12.5	13.0	13.5	14.0
82	245	147	45	15	5	3				
9	18	46	64	102	108	68	33	7	—	1
61	65	82	46	80	47	32	34	19		
09	173	161	103	53	34	5	2			
14	104	71	84	94	52	30	2			
82	59	65	65	98	81	41	13	2	1	
99	70	68	67	78	55	27	5			
41	64	106	97	122	78	64	16	9		
68	174	181	72	31	14	8	—	—	1	
86	109	109	62	73	41					
39	180	114	46	29	7	3	—	1		
53	110	89	47	53	29	9				
28	195	140	45	24	10	4	1			
24	157	116	49	52	14	1				
25	42	65	75	79	80	68	13	5		
76	167	128	71	50	26	17	3	1		
08	148	151	61	47	21	11	1	1	1	
20	66	49	26	18	7	3	2			
28	147	194	80	87	36	27	3	1		
77	178	179	75	56	28	9	1			
77	172	148	88	65	19	11	3			
91	108	112	92	90	69	31	20	4		
45	111	96	50	65	48	34	8	—	1	
58	96	50	14	5						
39	116	73	40	18	6					
13	168	128	102	67	26	14				
96	220	176	82	23	10					
58	187	143	101	44	25	11	5	6	3	
33	83	77	35	24	12	4	4	3	1	
13	84	97	43	29	9	4	5	2		
49	122	138	57	32	18	10	3	2	1	
39	121	85	37	27	13	4	5	7	2	
79	124	83	34	34	12	11	4	5	1	
74	130	92	37	21	9	12	3	2	3	

Table III (*continued*)

Year-class	Area	Date	Gear	No.	5.5	6.0	6.5	7.0	7.5	8.0	8
1960	07	12.11	PS	100							
		14.11	PS	100							
		18.11	PS	100							
	05	29.9	PS	266				9	48	62	
		20.10	PS	100		1	5	25	19	16	
		20.10	PS	1050			24	106	269	202	1
		30.10	PS	63					1	12	
	04	3.10	PS	126							
		23.10	PS	100				20	22	22	
		24.10	PS	97				1	2	16	
		24.10	PS	100					3	7	
		7.11	PS	1091				45	250	275	1
		16.11	PS	200				8	22	35	
		28.11	PS	100			1	6	6	8	
		29.11	PS	100					3	7	
		6.12	PS	100				1	2	1	
		14.12	PS	100				3	14	11	
	03	19.10	PS	131						8	
		21.10	PS	71							
		21.10	PS	100							
1961	07	31.1.62	PS	100							
		23.1.62	PS	100							
	06	16.12	PS	234							
		15.1.62	PS	90						1	
	05	4.9	PS	99					4	23	
		6.9	PS	100						5	
		27.9	PS	99							
	04	25.9	PS	100							
		25.10	PS	100						4	
		22.11	PS	95	1	4	9	11	14	13	
	03	20.9	PS	100							
		22.9	PS	30							

.0	9.5	10.0	10.5	11.0	11.5	12.0	12.5	13.0	13.5	14.0	14.5	15.0
2	8	9	14	22	16	18	6	2	2	1		
		2	7	9	16	20	18	15	9	3	1	
	1	3	16	15	21	22	12	6	1	3		
7	25	21	11	2								
6	3	3	3	4	1							
2	55	45	32	19	8	8	1					
3	5	9	4	1								
3	7	22	43	35	11	3	1	1				
2	4	1	1									
4	13	8	6	6	4							
8	24	14	7	6	5	1	1					
3	55	60	36	34	20	10						
9	18	18	9	9	7	3	—	—	1			
5	11	14	14	7	2							
3	7	8	14	20	13	4	3					
7	16	32	23	11								
3	13	3	8	12	8	2	1					
3	38	10	6	2	1							
		5	20	26	19	—	—	—	1			
3	12	39	27	13	6							
2	26	18	13	7	6	1	1					
		3	12	17	21	12	6	9	13	6	1	
	1	22	27	17	18	33	59	29	13	7	4	4
3	4	6	1	9	7	17	15	17	7	3		
9	10	4	1									
4	14	3	2									
5	18	19	24	19	10	1						
	8	24	32	26	9	1						
	17	18	7	9	5	5	2	—	2			
5	10	10	4	3	3							
	13	30	24	14	6	4						
	4	6	11	4	2	1						

Table III (*continued*)

Year-class	Area	Date	Gear	No.	4.5	5.0	5.5	6.0	6.5	7.0	7.5	8.0	8.5
1962	07	10.11	PS	100									
		20.11	PS	100									
		10.12	PS	318									
		12.12	PS	290									
		16.1.63	PS	100									
		24.1.63	PS	100									
	05	21.9	PS	200					1	3	20	30	35
		25.9	PS	162						1	25	70	47
		27.9	PS	200				4	7	14	32	48	46
	04	28.9	PS	210				18	63	87	25	8	3
		29.9	PS	224				3	5	6	17	20	30
		29.9	PS	186				5	7	10	22	22	28
	05	17.9	PT	55		1	8	13	16	4	5	6	1
		21.9	PT	102					3	4	6	11	22
		23.9	PT	102				2	6	13	30	29	14
		22.10	PT	101					1	3	15	26	30
	04	17.9	PT	100		1	3	16	20	24	18	14	3
		17.9	PT	109		4	19	42	31	9	3	—	—
		2.10	PT	102			1	4	5	15	19	21	16
		2.10	PT	99				3	3	11	14	11	11
		3.10	PT	103	1	1	2	14	18	23	14	8	8
		3.10	PT	64		1	5	15	11	7	4	5	11
		11.10	PT	100				4	6	5	9	15	17
		25.10	PT	100				1	1	9	17	15	15
		26.10	PT	104						1	1	6	14
		30.10	PT	100					3	9	7	17	19
		31.10	PT	100			1	4	21	18	26	11	11
		8.11	PT	100						4	9	14	16
		22.11	PT	101				3	5	8	10	12	13
		23.11	PT	107			2	—	6	10	11	19	18
		5.12	PT	103				2	5	10	19	20	13
	03	7.9	PT	54					3	5	6	12	25
		13.9	PT	52					1	2	4	9	21
		5.10	PT	101				3	9	22	34	14	10
		5.10	PT	101			1	1	7	25	27	23	12
		5.10	PT	87						2	1	4	15
		8.10	PT	22				1	—	2	9	4	4
		2.11	PT	80				1	5	8	19	9	21
		3.11	PT	19							4	4	2
		1.12	PT	81							1	2	6

.5	10.0	10.5	11.0	11.5	12.0	12.5	13.0	13.5	14.0	14.5	15.0	15.5	16.0
4	17	17	14	6	4	4	17	11	4	2			
	2	4	6	14	19	13	17	11	10	3	1		
		6	14	19	35	54	73	60	38	11	3	3	2
	5	9	27	33	37	42	47	48	28	10	3	1	
2	3	2	7	6	15	17	24	12	9	2			
		4	13	13	13	27	16	8	2	2	1	1	
7	22	19	7	1									
1	1	1	2										
3	7	1	1										
2	2	1											
3	42	21	2										
5	28	16	1	1									
7	5	1											
2	2												
3													
	1												
4	4	4	1										
5	11	7	2										
4	2	1	1										
5	9	7	4										
9	8	3	4										
3	20	20	8										
3	8	6	3	1									
	1	2											
5	11	1	4	1									
3	9	7	5	1	1	1							
9	6	1	2										
5	4	4	4	2	1								
2	1												
	1												
9	6	5											
3	3												
3	2												
	18	13	5	5	2	1							

Table III (*continued*)

Year-class	Area	Date	Gear	No.	4.5	5.0	5.5	6.0	6.5	7.0	7.
1963	05	5.9	PT	30						1	
		4.10	PT	100							
		16.11	PT	101			1	5	4	6	1
	04	9.9	PT	100				1	—	5	
		9.9	PT	84						2	
		9.9	PT	109						3	
		10.9	PT	101	1	38	40	17	3	—	
		20.9	PT	106		1	14	42	21	12	1
		20.9	PT	75		4	3	11	7	2	
		25.9	PT	34							
		26.9	PT	101					6	6	
		12.10	PT	11							
		30.10	PT	50						3	
		8.11	PT	102					2	11	
		14.11	PT	97							
		15.11	PT	100					1	5	
		20.11	PT	100					7	5	1
		4.12	PT	103				1	3	10	1
	03	18.9	PT	100							
		18.9	PT	51			3	4	4	4	
		20.9	PT	100							
		15.10	PT	65					3	9	1
		11.12	PT	101						1	

8.0	8.5	9.0	9.5	10.0	10.5	11.0	11.5	12.0	12.5	13.0	13.5
13	4	2	3	1							
	1	5	16	35	19	11	7	3	3		
22	14	11	8	9	2	3	3	1	1		
18	14	21	15	14	3	2					
8	11	27	15	11	2	1					
18	18	34	23	6	1						
—	1										
2	1	—	—	—	1						
5	11	9	8	4	4	2	2				
			1	3	12	12	3	3			
4	5	7	13	14	19	15	5	2	1		
		1	—	1	1	3	4	1			
5	2	5	4	8	5	6	6	2	1	1	
9	7	8	12	23	10	7	3	1			
	3	2	9	9	13	28	18	11	3	1	
1	5	13	15	21	16	13	5	2			
12	13	11	12	11	7	5	3	2			
10	9	6	6	10	11	11	7	5	1	1	
		6	29	30	28	7					
2	3	11	6	7	4	1					
10	22	24	27	15	2						
5	—	1	—	2	8	9	7	6	3	1	
2	3	4	14	20	19	18	8	5	2	1	

Table III (*continued*)

Year-class	Area	Date	Gear	No.	4.0	4.5	5.0	5.5	6.0	6.5	7.0	7
1964	04	9.9	PT	100				2	10	24	19	
		10.9	PT	100			1	4	28	31	19	
		21.9	PT	100					3	8	31	
		21.9	PT	101				1	8	13	25	
		27.9	PT	96				1	—	6	23	
		28.9	PT	100					1	5	16	
		9.10	PT	101	1	—	—	—	—	1	1	
		9.10	PT	65								
		22.10	PT	52	1	6	1	1	2	7	10	
		10.11	PT	53								
		12.11	PT	34							1	
		18.11	PT	100			1	1	2	17	39	
		18.11	PT	100					2	11	20	
		18.11	PT	100							3	
		20.11	PT	103								
		10.12	PT	101			1	1	—	5	9	
		11.12	PT	12								
		18.12	PT	100								
	03	15.9	PT	100						6	23	
		15.9	PT	100						7	25	
		18.9	PT	101							5	
		18.9	PT	101			1	2	7	20	23	
		21–22.9	PT	100							4	
		19.11	PT	22			1	—	—	—	—	
		9.12	PT	102						2	14	
	02	21.9	PT	29								
	10	13.9	PT	103					4	3	1	
		14.9	PT	102				2	16	43	27	
	13	11.9	PT	60						1	5	
		22.9	PT	100					2	13	14	
		23.9	PT	68					1	4	7	
	12	9.9	PT	53					2	3	5	
		10.9	PT	101							1	
		23.9	PT	100			1	3	3	5	7	
		24.9	PT	108					2	3	7	
		26.9	PT	100				3	10	17	18	

8.0	8.5	9.0	9.5	10.0	10.5	11.0	11.5	12.0	12.5	13.0	13.5
13	9	5	2	1	1						
4	2	1	—	—	1						
13	5	1	2	1							
13	8	5	1	1							
15	16	2	6	—	—	1					
17	1										
16	16	15	8	12	10	11	2	1			
1	1	2	1	7	10	20	13	9	1		
5	2	2	1								
	2	3	1	4	12	15	12	3	1		
3	1	1	4	4	3	8	4	3			
9	11	3									
16	14	3	4	3	1						
5	9	20	25	17	2	4	5	3	2		
20	16	14	5	12	8	6	7	—	1		
14	16	8	6	4	1	6	5	4	4	4	
					1	2	2	4	1	1	1
3	—	3	3	12	19	23	19	8	4	4	
14	7	8	9	3	4						
13	9	13	8	3	4	1					
41	15	7	4	2	1						
17	6	2	2								
14	24	12	21	10	5	3	1				
4	6	5	3								
24	8	7	4	2	3	2	1	1	1	1	
1	1	2	6	8	6	3	2				
4	26	32	19	8	4	1					
2	1	1									
29	13										
27	6	9	4	3	2						
15	12	8	2	3	4	—	—	1			
14	7	6	4	3	2						
1	7	15	27	24	22	3					
13	3	11	15	14	6	3	2				
29	13	12	10	8	3	1					
20	6	3	2	1	1						

Table IV. Analysis of variance of the data in Table III.

Area	Gear	Source of variation	Sums of squares	Degrees of freedom	Variance of estimate	F	Probability
					1959 year-class		
		Between areas	10631.302	2	5315.651 (s^2_B)		
		Within areas	122725.400	25615	4.791 (s^2_W)		
05, 04 and 03	PS	Between samples	19181.219	31	618.749 (s^2_b)	$\frac{s^2_b}{s^2_w}$	<0.05
		Within samples	103544.181	25584	4.047 (s^2_w)		
		Total	133356.702	25617		$\frac{s^2_B}{s^2_b}$	<0.05
					1960 year-class		
		Between areas	3024.802	2	1512.401 (s^2_B)		
		Within areas	21462.832	3892	5.515 (s^2_W)		
05, 04 and 03	PS	Between samples	4563.484	14	325.963 (s^2_b)	$\frac{s^2_b}{s^2_w}$	<0.05
		Within samples	16899.348	3878	4.358 (s^2_w)		
		Total	24487.634	3894		$\frac{s^2_B}{s^2_b}$	<0.05
		Between areas	12068.346	3	4022.782 (s^2_B)		
		Within areas	22768.419	4191	5.433 (s^2_W)		
07, 05, 04 and 03	PS	Between samples	4761.771	16	297.611 (s^2_b)	$\frac{s^2_b}{s^2_w}$	<0.05
		Within samples	18006.648	4175	4.312 (s^2_w)		
		Total	34836.765	4194		$\frac{s^2_B}{s^2_b}$	<0.05
					1961 year-class		
		Between areas	341.263	2	170.632 (s^2_B)		
		Within areas	3852.209	720	5.350 (s^2_W)		
05, 04 and 03	PS	Between samples	1589.416	5	317.883 (s^2_b)	$\frac{s^2_b}{s^2_w}$	<0.05
		Within samples	2262.793	715	3.165 (s^2_w)		

				1961 year-class		
		Between areas	5563.961	4	1390.990 (s^2_B)	
		Within areas	7530.480	1242	6.063 (s^2_W)	
07, 06, 05, 04 and 03	PS	Between samples	2486.318	7	355.188 (s^2_b)	$\frac{s^2_b}{s^2_w}$ <0.05
		Within samples	5044.162	1235	4.084 (s^2_w)	
		Total	13094.441	1246		$\frac{s^2_b}{s^2_B}$ >0.05
				1962 year-class		
		Between areas	75.579	1	75.579 (s^2_B)	
		Within areas	6567.199	1180	5.565 (s^2_W)	
05 and 04	PS	Between samples	2373.214	4	593.304 (s^2_b)	$\frac{s^2_b}{s^2_w}$ <0.05
		Within samples	4193.985	1176	3.566 (s^2_w)	
		Total	6642.778	1181		$\frac{s^2_B}{s^2_b}$ >0.05
		Between areas	130.997	2	65.499 (s^2_B)	
		Within areas	16210.148	2446	6.627 (s^2_W)	
05, 04 and 03	PT	Between samples	6826.211	25	273.048 (s^2_b)	$\frac{s^2_b}{s^2_w}$ <0.05
		Within samples	9383.937	2421	3.876 (s^2_w)	
		Total	16341.145	2448		$\frac{s^2_B}{s^2_b}$ >0.05
		Between areas	38258.607	2	19129.303 (s^2_B)	
		Within areas	11960.318	2187	5.469 (s^2_W)	
07, 05 and 04	PS	Between samples	2908.844	9	323.205 (s^2_b)	$\frac{s^2_b}{s^2_w}$ <0.05
		Within samples	9051.474	2178	4.156 (s^2_w)	
		Total	50218.925	2189		$\frac{s^2_B}{s^2_b}$ <0.05

Table IV (*continued*)

Area	Gear	Source of variation	Sums of squares	Degrees of freedom	Variance of estimate	F	Probability
					1963 year-class		
		Between areas	858.072	2	429.036 (s^2_B)		
		Within areas	22565.678	1918	11.765 (s^2_W)		
05, 04 and 03	PT	Between samples	11912.946	20	595.647 (s^2_b)	$\frac{s^2_b}{s^2_w}$	<0.05
		Within samples	10652.732	1898	5.613 (s^2_w)		
		Total	23423.750	1920		$\frac{s^2_B}{s^2_b}$	>0.05
					1964 year-class		
		Between areas	205.966	1	205.966 (s^2_B)		
		Within areas	21332.571	2142	9.959 (s^2_W)		
04 and 03	PT	Between samples	12011.093	23	522.221 (s^2_b)	$\frac{s^2_b}{s^2_w}$	<0.05
		Within samples	9321.478	2119	4.399 (s^2_w)		
		Total	21538.537	2143		$\frac{s^2_B}{s^2_b}$	>0.05
		Between areas	400.601	4	100.150 (s^2_B)		
		Within areas	27509.570	3063	8.981 (s^2_W)		
04, 03, 02, 10, 13 and 12	PT	Between samples	14636.416	31	472.142 (s^2_b)	$\frac{s^2_b}{s^2_w}$	<0.05
		Within samples	12873.154	3032	4.246 (s^2_w)		
		Total	27910.171	3067		$\frac{s^2_B}{s^2_b}$	>0.05

Table V. Mean length of 0-group herring of the 1959–1965 year-classes caught with pelagic trawl (PT), purse seine (PS) and Isaacs–Kidd ten foot midwater trawl (IKMT).

Year-class	Date of sampling	Area	Gear	No. of samples	No. of fish	Mean length in cm.	Standard deviation	Standard error
1959	28.9	06	PT	1	101	11.6	0.86	0.09
	6.10	05	PT	1	102	9.2	1.28	0.13
	1.10–16.11	05	PS	3	300	10.2	1.15	0.07
	13.10–27.11	04	PT	5	441	7.5	1.23	0.06
	8.10–2.12	04	PS	20	1993	9.7	0.35	0.01
	18.10–1.12	03	PS	11	1104	9.2	1.04	0.03
	16.10	02	Stomach content	1	9	7.8	1.25	0.42
	8.10	13	Stomach content	1	15	8.6	0.71	0.18
	12.10	15	Stomach content	2	24	8.1	1.42	0.29
1960	12–18.11	07	PS	3	300	11.6	1.04	0.06
	18–29.11	06	PS	2	106	9.8	1.01	0.10
	29.9–2.10	05	PT	2	56	8.5	1.04	0.14
	28–29.9	05	IKMT	5	359	7.3	0.70	0.04
	29.9–30.10	05	PS	4	362	8.4	1.08	0.06
	2.10–30.11	04	PT	5	217	8.4	1.28	0.09
	3.10–14.12	04	PS	10	1001	9.4	1.29	0.04
	10.10–11.11	03	PT	4	371	8.6	1.08	0.06
	19–21.10	03	PS	3	273	10.1	0.93	0.06
	14.10	02	PS	1	100	9.4	0.77	0.08
	13.10	10	PS	1	100	9.3	0.70	0.09
	13.10	13	PT	1	59	9.7	0.62	0.08
	12.10	15	PT	1	53	8.7	0.89	0.12
	22.9–5.10	20	PT	3	301	7.9	0.65	0.04
	21.9–8.10	20	IKMT	4	285	7.5	0.80	0.05
	7.10	20	PS	1	100	7.2	0.42	0.04

Table V (*continued*)

Year-class	Date of sampling	Area	Gear	No. of samples	No. of fish	Mean length in cm.	Standard deviation	Standard error
1961	13–23.1.62	07	PS	2	200	10.9	1.47	0.10
	16.12.61–15.1.62	06	PS	2	190	12.0	1.26	0.09
	4–27.9	05	PT	4	329	8.4	0.87	0.05
	4–27.9	05	PS	3	298	9.3	0.94	0.03
	24.9–21.11	04	PT	13	1229	8.5	1.34	0.04
	25.9–22.11	04	PS	3	295	9.6	1.46	0.08
	21.9–10.12	03	PT	8	726	8.8	1.33	0.05
	20–22.9	03	PS	2	130	10.3	0.75	0.07
	17–20.9	10	PT	4	101	9.2	0.90	0.09
	9–10.9	12 and 20	PT and PS	2	10	9.0	1.62	0.51
1962	10.11.62–16.1.63	07	PS	2	200	12.0	1.36	0.10
	21.12	06	PS	1	98	10.9	0.87	0.09
	17.9–22.10	05	PT	4	360	8.0	1.03	0.05
	21–27.9	05	PS	3	308	8.5	0.95	0.05
	17.9–5.12	04	PT	15	1492	8.1	1.40	0.04
	28–29.9	04	PS	3	302	8.2	1.37	0.08
	7.9–1.12	03	PT	9	597	8.3	1.12	0.05
	7.9	10	PT	2	108	8.1	0.59	0.06
	8.9	13	PT	1	99	7.8	0.75	0.08
1963	24.10–10.12	07	PS	3	302	11.5	1.27	0.07
	15.12	06	PT	1	99	10.0	1.29	0.13
	5.9–16.11	05	PT	3	231	9.5	1.44	0.09
	4.10	05	PS	1	100	9.7	0.96	0.10
	9.9–4.12	04	PT	15	1273	9.0	1.87	0.05

1963	27.9–13.11	04	PS	3	301	10.3	1.34	0.08
	18.9–11.12	03	PT	5	417	9.8	1.34	0.07
	20.9	10	PT	1	79	7.9	0.75	0.08
	5.8	12	PT	1	102	5.8	0.65	0.06
	24.9	20	PT	1	100	7.6	0.51	0.05
1964	7.12	07	PS	1	101	13.8	1.11	0.11
	30.10–3.12	06	PS	2	200	10.4	1.28	0.09
	1.10	05	PT	1	100	9.3	0.52	0.05
	9.9–18.12	04	PT	18	1518	8.7	1.73	0.04
	29.9	04	PS	2	200	9.2	1.06	0.07
	15.9–29.12	03	PT	7	626	8.3	1.11	0.05
	16–25.9	03	PS	2	200	10.0	0.72	0.05
	21.9	02	PT	1	29	10.3	0.82	0.15
	13–14.9	10	PT	2	205	8.0	1.34	0.09
	11–23.9	13	PT	3	228	8.2	0.95	0.06
	23.9	15	PT	1	20	8.3	1.05	0.23
	9–26.9	12	PT	5	462	8.7	1.34	0.06
	2.9	20	PT	1	46	7.8	0.64	0.09
	4–6.9	21	PT	2	40	6.7	0.57	0.09
1965	14.10–16.11	07	PS	3	298	12.6	1.62	0.09
	25–27.8	05	PT	2	161	6.4	1.35	0.11
	30.8	04	PT	2	258	5.1	0.39	0.02
	9–14.9	12	PT	2	47	8.8	1.24	0.18
	10–11.9	21	PT	2	96	6.6	0.76	0.08

Table VI. Mean annual length increments (t in cm) of herring (1959 year-class) collected in different regions in 1961–1965, s = standard deviation and $s/\sqrt{n}$ = standard error.

Region	Date		n	$\bar{t}_1$	s_1	$s_1/\sqrt{n}$	$\bar{t}_2$	s_2	$s_2/\sqrt{n}$	$\bar{t}_3$	s_3	$s_3/\sqrt{n}$	$\bar{t}_4$	s_4	$s_4/\sqrt{n}$
Off Vesterålen	1961	24.8–6.9	116	9.44	1.62	0.15	7.71	1.34	0.12						
Off Torsvåg		12–22.9	166	8.88	1.00	0.08	7.21	1.01	0.08						
Off North Cape		11–22.9	89	8.03	0.97	0.10	6.63	0.86	0.09						
Off eastern Finnmark		20.9	30	7.05	0.72	0.13	5.83	0.89	0.16						
Off eastern Finnmark	1962	18.2–6.3	32	7.64	1.00	0.18	5.63	1.02	0.18						
Off Iceland		21.7–14.9	100	8.82	1.30	0.13	7.11	1.01	0.10						
Off Torsvåg		18–29.9	237	7.69	1.20	0.08	6.22	0.98	0.06	4.38	1.19	0.08			
Off Finnmark		1.7–2.8	391	7.53	0.96	0.05	5.99	0.98	0.05	3.86	0.80	0.04			
Off eastern Finnmark		13.9–5.11	51	7.74	1.08	0.15	5.57	0.83	0.12	3.77	0.70	0.10			
Off Iceland	1963	29.7–14.8	102	9.16	1.41	0.14	7.39	1.18	0.12	6.66	1.54	0.15	4.40	1.21	0.12
Off Torsvåg		1–30.10	130	7.58	1.24	0.11	6.21	1.15	0.10	4.18	1.31	0.11	4.33	1.33	0.12
Off Møre	1964	17–20.2	107	9.46	1.15	0.11	6.84	1.19	0.12	5.92	1.68	0.16	4.75	1.33	0.13
Off Lofoten		2–4.3	106	8.17	1.10	0.11	6.46	1.02	0.10	4.94	1.64	0.16	4.81	1.31	0.13
Off Møre	1965	15.2	96	8.30	1.41	0.14	6.79	1.31	0.13	5.32	1.59	0.16	4.99	1.41	0.14
Off Lofoten		18–20.2	99	8.10	1.32	0.13	6.06	1.20	0.12	4.47	1.53	0.15	4.87	1.51	0.15

Table VII. Catch of 0- and I-group herring of the 1959 and 1960 year-classes landed by purse seiners in different areas.

Year-class	Month	Area	Catch in tons	No. of vessels
1959	November	05 and 04	6178	29
	December	05 and 04	5699	26
	January	05 and 04	2466	19
	February	05 and 04	887	12
	March	05 and 04	4	1
	April	05 and 04	262	4
	November	05, 04 and 03	6636	14
	December	05, 04 and 03	4330	13
	January	05, 04 and 03	4403	16
	February	05, 04 and 03	685	6
	March	05, 04 and 03	1647	10
	April	05, 04 and 03	1041	11
1960	December	05 and 04	7556	41
	January	05 and 04	6742	34
	February	05 and 04	2256	19
	March	05 and 04	689	7
	April	05 and 04	264	5
	December	05, 04 and 03	9728	23
	January	05, 04 and 03	11647	25
	February	05, 04 and 03	1612	17
	March	05, 04 and 03	580	4
	April	05, 04 and 03	1786	18

Table VIII. Catch and average weight of young and adolescent herring (1959 year-class) accordi to month and district.

Month	Møre and Romsdal, Trøndelag		Nordland		Troms		Finnmark	
	Catch in tons	Weight in g	Catch in tons	Weight in g	Catch in tons	Weight in g	Catch in tons	Weigh in g
				0- and I-group				
October	11979	11	13982	9	1963	7	2310	5
November	14579	11	19275	9	5289	7	20108	5
December	303	11	10123	9	10946	7	14527	5
January	313	11	3595	9	10072	7	15173	5
February	—	—	237	9	3155	7	1567	5
March	44	13	59	9	487	7	9072	5
April	1373	16	458	11	424	9	4487	6
				I- and II-group				
May	9693	22	2744	15	3395	13	4797	7
June	7045	32	1962	23	399	18	2816	9
July	1280	43	1148	34	716	24	8698	11
August	8986	57	764	46	59	34	1447	16
September	3667	63	1088	48	3	40	—	—
October	2552	66	3987	49	146	43	—	—
November	3437	67	1990	49	1309	44	3795	21
December	1324	67	495	49	1401	44	8075	21
January	937	67	2141	49	1453	44	7616	21
February	56	67	776	49	556	44	1898	21
March	1	68	104	49	109	44	1137	21
April	345	73	296	50	270	44	2052	22
				II- and III-group				
May	3429	82	309	53	573	45	947	24
June	3523	91	395	63	749	47	14702	29
July	1798	101	176	77	368	57	35997	34
August	1800	112	4421	93	309	76	38	41
September	526	123	3263	98	69	90	50	47
October	759	132	6393	99	1682	96	18	51
November	749	138	2943	100	1013	99	46	53
December	961	140	1444	100	514	100	13	54
January	161	140	1621	100	340	100	—	—
February	15	140	254	100	37	100	—	—
March	22	140	28	100	—	—	—	—
April	60	140	5	100	—	—	—	—

ble IX. Catch and average weight of young and adolescent herring (1963 year-class) according to month and district.

Month	Møre and Romsdal, Trøndelag		Nordland		Troms		Finnmark	
	Catch in tons	Weight in g	Catch in tons	Weight in g	Catch in tons	Weight in g	Catch in tons	Weight in g
				0- and I-group				
tober	6220	11	1673	9	1316	7	449	5
vember	4248	11	11031	9	9051	7	1770	5
cember	1303	11	1606	9	374	7	386	5
nuary	563	11	4018	9	261	7	7	5
bruary	—	—	—	—	—	—	—	—
arch	—	—	—	—	—	—	—	—
ril	—	—	161	11	—	—	—	—
				I- and II-group				
ay	1199	22	934	15	1039	13	506	7
ne	2103	32	1120	23	837	18	235	9
ly	1300	43	583	34	204	24	8	11
gust	1071	57	726	46	11	34	—	—
ptember	854	63	1374	48	3	40	—	—
tober	1120	66	4552	49	322	43	—	—
vember	1429	67	3868	49	856	44	1409	21
cember	524	67	834	49	261	44	2814	21
nuary	173	67	338	49	171	44	2663	21
bruary	35	67	—	—	—	—	—	—
arch	222	68	—	—	—	—	—	—
ril	259	73	44	50	1	44	—	—
				II- and III-group				
ay	6664	82	1486	53	1019	45	615	24
ne	1898	91	1482	63	711	47	5315	29
ly	1787	101	4714	77	1150	57	38480	34
gust	1716	112	7934	93	832	76	19154	41
ptember	718	123	3535	98	2664	90	5953	47
tober	1106	132	1162	99	108	96	1346	51
vember	563	138	825	100	11	99	363	53
cember	219	140	162	100	—	—	23	54
nuary	—	—	—	—	—	—	—	—
bruary	—	—	—	—	—	—	—	—
arch	—	—	—	—	—	—	—	—
ril	47	140	2	100	—	—	—	—

Table X. Catch and average weight of young and adolescent herring (1959 year-class) according month and district.

Month	Møre and Romsdal, Trøndelag		Nordland		Troms		Finnmark	
	Catch in tons	Weight in g	Catch in tons	Weight in g	Catch in tons	Weight in g	Catch in tons	Weig in g
				III- and IV-group				
May	57	141	357	100	—	—	—	—
June	57	143	2439	101	141	101	8059	55
July	21	147	232	103	227	102	58948	56
August	27	157	9955	108	235	104	3543	62
September	11	172	7852	113	1173	107	—	—
October	11	199	9606	123	954	112	—	—
November	60	199	2974	131	391	117	—	—
December	14	199	1858	131	8	117	—	—
January	—	—	904	131	—	—	—	—
February	—	—	303	131	—	—	—	—
March	—	—	149	131	—	—	—	—
April	8	199	859	131	—	—	—	—
				IV- and V-group				
May	45	199	999	140	13	123	—	—
June	99	200	643	155	6312	135	7426	85
July	74	200	6277	180	1506	160	9245	90
August	113	200	3751	200	13	180	275	100
September	48	200	238	200	22	200	11	120
October	43	200	356	200	655	200	1121	140
November	39	200	332	200	—	—	60	140
December	19	200	20	200	18	200	—	—
January	3	200	12	200	—	—	44	140
February	—	—	—	—	—	—	—	—
March	—	—	—	—	—	—	—	—
April	249	200	2951	200	—	—	—	—
				V-group				
May	—	—	33	200	7	200	—	—
June	—	—	49	200	4	200	—	-
July	—	—	67	200	1	200	—	—
August	—	—	79	200	2	200	—	—
September	—	—	—	—	—	—	—	—
October	—	—	—	—	—	—	—	—
November	—	—	—	—	—	—	—	—
December	45	225	305	200	155	200	—	-

ble XI. Catch and average weight of young and adolescent herring (1963 year-class) according to month and district.

Month	Møre and Romsdal, Trøndelag*		Nordland*		Troms		Finnmark	
	Catch in tons	Weight in g	Catch in tons	Weight in g	Catch in tons	Weight in g	Catch in tons	Weight in g
				III- and IV-group				
ıy	195	141	8	100	—	—	660	54
ıe	97	143	29	101	—	—	9972	55
y	24	147	37	103	1	102	34656	56
gust	26	157	18	108	8	104	27557	62
ɔtember	14	172	16	113	3	107	16943	72
tober	16	199	27	123	12	112	6	79
vember	24	199	7	131	—	—	—	—
cember	5	199	—	—	—	—	—	—
ıuary	—	—	—	—	26	117	12	81
ɔruary	—	—	—	—	—	—	—	—
ırch	—	—	—	—	—	—	—	—
ril	—	—	—	—	—	—	19778	81
				IV- and V-group				
ıy					2	123	3046	83
ıe					22	135	7998	85
y					6	160	10312	90
gust					11	180	8655	100
ɔtember					431	200	1426	120
tober					520	200	606	140
vember					207	200	323	140
cember					20	200	105	140
ıuary					—	—	—	—
ɔruary					—	—	—	—
ırch					—	—	—	—
ril					—	—	—	—
				V-group				
ıy					—	—	8380	140
ıe					—	—	41900	140
y					—	—	41900	140
gust					6	200	29330	140
ɔtember					30	200	—	—
tober					30	200	—	—
vember					—	—	—	—
cember					—	—	—	—

* Data incomplete.

Table XII. Estimated annual yields which might have been obtained from the 1959 and 1963 ye classes by refraining from fishing 0- to III-group herring, and by starting the exploitation at six ye of age (calculated from 1 January). $M_1 = 2.76$, $M_2 = 1.38$ and two alternative values of $M_3 =$ $= M_5 = M_6$, i.e. 0.16 and 0.24 have been used to estimate N_6. Average values of $E = 0.64$ a $Z = 0.44$ are used for the period of exploitation (Anon. 1969).

Year	Average weight in g	Alternative 1			Alternative 2		
		No. by 1 Jan. $\times 10^{-6}$ N_n	Catch in no. $\times 10^{-6}$ C_n	Catch in thousands of metric tons	No. by 1 Jan. $\times 10^{-6}$ N_n	Catch in no. $\times 10^{-6}$ C_n	Catch in thousand of metri tons
1965	225	3959	902	203	2970	677	152
1966	242	2550	581	141	1912	436	105
1967	293	1642	374	110	1232	281	82
1968	302	1058	241	73	793	181	55
1969	317	681	155	49	511	116	37
1970	321	439	100	32	329	75	24
1971	334	282	64	21	212	51	17
1972	341	182	41	14	136	31	11
1973	364	117	27	10	88	20	7
1974	388	75	17	7	57	13	5
1975	388	49	11	4	36	8	3
1976	388	31	7	3	23	5	2
1977	388	20	5	2	15	3	1
Total		11085	2525	669	8314	1897	501
1969	225	1998	455	102	1514	345	78
1970	242	1287	293	71	975	222	54
1971	293	829	189	55	628	143	42
1972	302	534	122	37	404	92	28
1973	317	344	78	25	260	59	19
1974	321	221	50	16	168	38	12
1975	334	143	32	11	108	25	8
1976	341	92	21	7	70	16	5
1977	364	59	13	5	45	10	4
1978	388	38	9	3	29	7	3
1979	388	25	6	2	19	4	2
1980	388	16	4	1	12	3	1
1981	388	10	2	1	8	2	1
Total		5596	1274	336	4240	966	257

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FURTHER STUDIES ON BLOOD PROTEIN POLYMORPHISM IN SPRAT

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INTRODUCTION

Polymorphism of hemoglobins and serum transferrins of sprat, *Sprattus sprattus* (L.), has been described on basis of 28 samples from the Norwegian coast (Nævdal 1968). Reliability of the type determinations, heredity and choice of characteristic sample parameters were discussed, and significant differences, especially among the samples from western Norway, were noted. The purpose of the present study has been to compare sprat from the Norwegian coast to the sprat population at its potential origin areas (see Dannevig 1951 for references).

MATERIAL AND METHODS

Sampling and treatment of hemoglobins and sera, analyses by electrophoresis, staining of proteins, etc. were performed in the same way as described by Nævdal (1968). Sampling localities are shown in Fig. 1 and listed in Table I together with sampling dates and numbers of specimens determined for hemoglobin and serum transferrin types. Samples collected at the same place on the same day were taken from different catches. Numbers in brackets indicate unreliable results due to aging or warming of the samples before the analyses. These results have been omitted in the discussion.

The age of the sprat was determined partly from size and partly from growth zones in the otoliths.

RESULTS AND DISCUSSION

Distributions of hemoglobin types in the 1967 and 1968 samples are shown in Table 1 (Norwegian coast) and Table 2 (North Sea and Kattegat). The type HbI-1-3 was not found in these samples. Corresponding distributions of transferrin types are shown in Table 3 and Table 4.

The distributions and the diagram of the 95 per cent limits of confidence (Fig. 2) show good agreement between the results from the samples

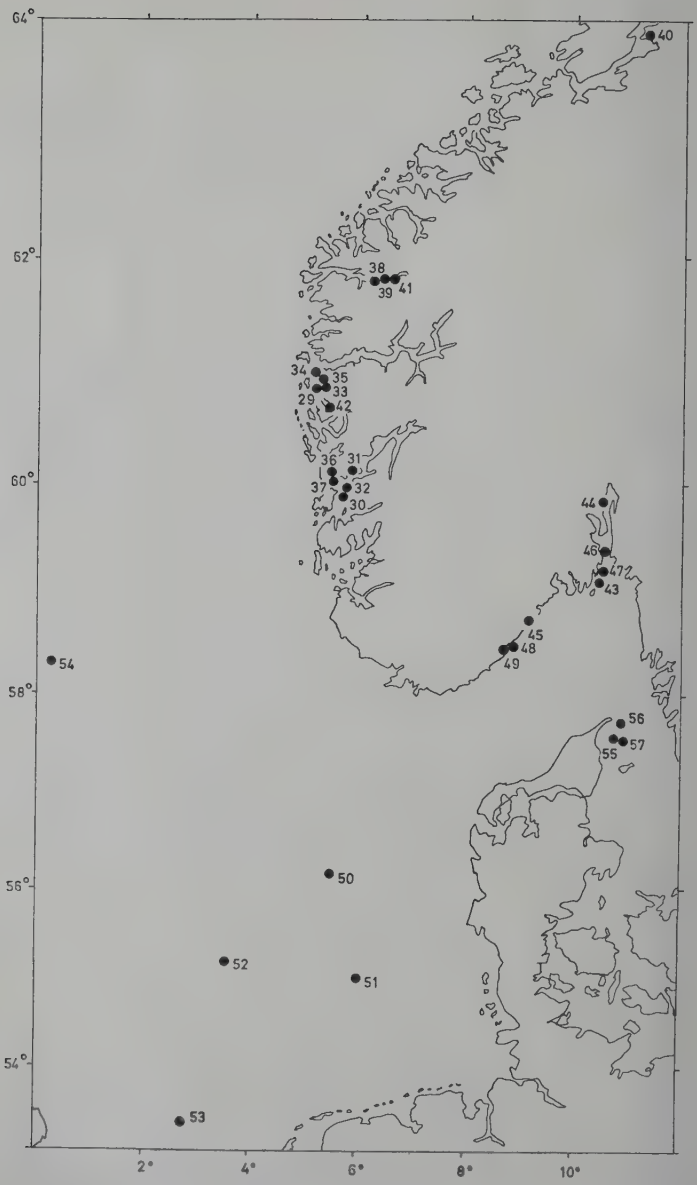

Fig. 1. Sampling localities of blood samples of sprat in 1967 and 1968.

Table 1. Distribution of hemoglobin patterns (phenotypes) in samples of sprat from the Norwegian coast 1967 and 1968.

Sample no.	Hemoglobin patterns					No.	Frequency of pattern HbI-1
	HbI-1	HbI-1-2	HbI-2-3	HbI-3	HbI-2		
29	82	24	1	2	3	110	74.5
30	92	8	—	—	—	100	92.0
31	81	6	—	—	1	88	92.5
32	96	8	—	—	—	104	92.3
33	105	14	—	—	4	123	85.4
34	92	10	—	1	2	105	87.6
35	75	19	2	—	1	97	77.3
36	79	22	—	—	3	104	76.0
37	74	24	4	1	1	104	71.2
38	66	11	—	1	—	78	84.6
39	70	9	—	1	—	80	87.5
40	58	4	—	—	—	62	93.5
41	83	9	—	—	1	93	89.2
42	64	18	1	2	6	91	70.3
43	34	13	—	—	3	50	68.0
44	43	10	—	—	2	55	78.2
45	69	8	—	—	1	78	87.2
47	93	2	—	—	—	95	97.9
48	118	2	—	—	—	120	98.3
49	113	5	—	—	—	118	95.8

collected in 1967 and 1968 from the Norwegian coast and the results from previous years. Great variations were observed among samples, especially among samples from western Norway.

High value of HbI-1 frequencies and intermediate values of q_A characterized the samples from Kattegat. Fig. 2 shows that part of the samples from western Norway, most of the samples from the Skagerak coast and one sample from the Oslo fjord coincided with the Kattegat samples. Most of the samples from the North Sea also showed high value of HbI-1 frequencies while some had higher q_A values than the Kattegat samples. These results were also in accordance with the results of a few of the samples collected at the Norwegian coast. However, a considerable part of the samples collected at the coast had conformity neither with the samples from Kattegat nor with the samples from the North Sea. This is illustrated in Fig. 3 where both the q_A-values and the HbI-1 frequencies for each sample are plotted in a scattering diagram. Samples with less than 50 reliable determinations of specimens have been omitted, but the previous samples (NÆVDAL 1968) are included.

The most likely explanation of the variation among samples is that the samples are collected from populations which differ in their gene pool,

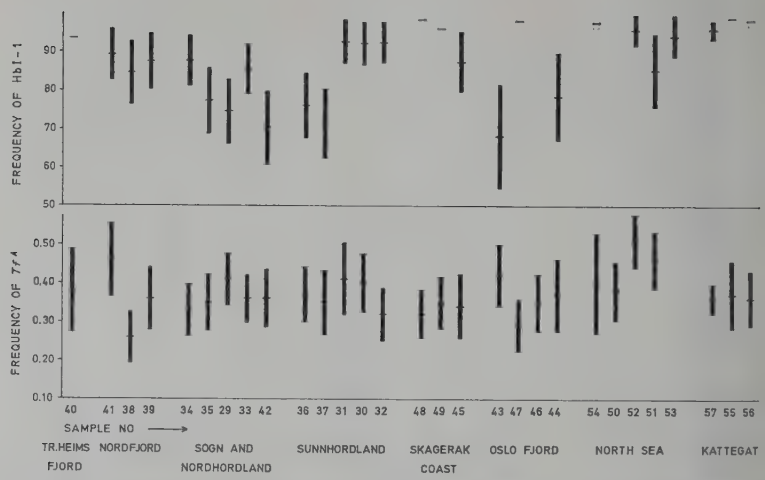

Fig. 2. Confidence intervals for the universal frequencies of HbI-1 and for the gene Tf^{A} supposed to control the transferrins in the Tf A-group. Horizontal lines mark the observed frequencies, and the vertical bars show the 95% confidence limits. The samples are arranged in geographical order.

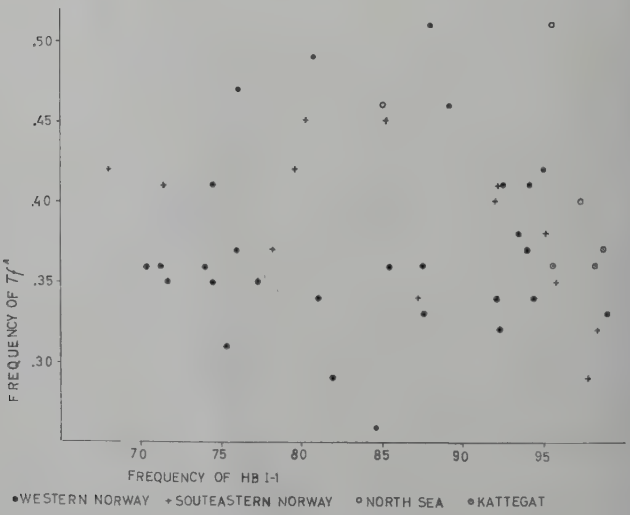

Fig. 3. Relation between frequencies of the hemoglobin type HbI-1 and the transferrin gene Tf^{A} in sprat samples. Samples of less than 50 specimens are omitted in the diagram.

Table 2. Distributions of hemoglobin pattern in samples of sprat from the North Sea and Kattegat.

Sample no.	Hemoglobin patterns					No.	Frequency of pattern HbI-1
	HbI-1	HbI-1-2	HbI-2-3	HbI-3	HbI-2		
51	51	8	—	—	1	60	85.0
52	106	5	—	—	—	111	95.5
53	77	3	—	—	2	82	93.9
54	109	3	—	—	—	112	97.3
55	74	1	—	—	—	75	98.7
56	112	2	—	—	—	114	98.2
57	307	12	—	—	2	321	95.6

that is populations which are reproductively separated. The results therefore indicate that a major part of the sprat in Norwegian waters may be recruited from spawning grounds in the Kattegat. Recruitement from the North Sea may also account for a part of the Norwegian sprat population. The origin of the sprat from which the rest of the samples have been taken, is not clear, but local populations in the fjords may be one explanation. It is also possible that the samples from Kattegat and the North Sea are not representative for these areas, and that other sprat populations exist from which no samples have been taken.

It is evident that no covariance exists between the observed pair of values (Fig. 3). This implies that more than two separated populations have been sampled, although some of the samples may represent a mixture of specimens of different origin. The mechanism which prevents gene flow between the populations, is still unknown.

The results of the studies on blood proteins of sprat indicate the following conclusion: the sprat population in Norwegian coastal waters consists of a major group recruited from spawning grounds in the Kattegat and the North Sea and minor groups recruited from local populations in the fjords.

SUMMARY

1. About 3000 specimens comprising 29 samples of sprat have been analysed for hemoglobin and serum protein types. The samples were collected at different localities on the Norwegian coast, in Kattegat and the North Sea.
2. The results of the samples from the coast confirm the results obtained by corresponding studies made before, i.e. great variations among samples, especially among samples from western Norway.

Table 3. Observed distributions of transferrin groups in samples of sprat from the Norwegian coast compared to expected Hardy-Weinberg distributions.

Sample no.		Transferrin groups			No.	q_A	χ^2	Probability of worse fit
		Tf AA	Tf AB	Tf BB				
29	obs	15	57	35	107	0.41		
	exp	18.0	51.8	37.2	107.0		1.15	$0.2 < P < 0.3$
30	obs	16	35	33	84	0.40		
	exp	13.4	40.3	30.2	83.9		1.46	$0.2 < P < 0.3$
31	obs	9	27	19	55	0.41		
	exp	9.2	26.6	19.1	54.9		0.01	$0.90 < P < 0.95$
32	obs	11	38	45	94	0.32		
	exp	9.6	40.9	43.5	94.0		0.46	$0.3 < P < 0.5$
33	obs	17	55	52	124	0.36		
	exp	16.1	57.1	50.8	124.0		0.16	$0.5 < P < 0.7$
34	obs	11	44	46	101	0.33		
	exp	11.0	44.7	45.3	101.0		0.02	$0.8 < P < 0.9$
35	obs	11	38	36	85	0.35		
	exp	10.4	38.7	35.9	85.0		0.05	$0.8 < P < 0.9$
36	obs	11	46	34	91	0.37		
	exp	12.5	42.4	36.1	91.0		0.61	$0.3 < P < 0.5$
37	obs	7	33	28	68	0.35		
	exp	8.3	30.9	28.7	67.9		0.36	$0.5 < P < 0.7$
38	obs	5	33	44	82	0.26		
	exp	5.5	31.6	44.9	81.9		0.13	$0.7 < P < 0.8$
39	obs	9	33	29	71	0.36		
	exp	9.2	32.7	29.1	71.0		0.01	$0.90 < P < 0.95$
40	obs	4	22	14	40	0.38		
	exp	5.8	18.8	15.4	40.0		1.23	$0.2 < P < 0.3$
41	obs	10	32	14	56	0.46		
	exp	11.8	27.8	16.3	55.9		1.22	$0.2 < P < 0.3$
42	obs	14	31	37	82	0.36		
	exp	10.6	37.8	33.6	82.0		2.65	$0.1 < P < 0.2$
43	obs	16	34	28	78	0.42		
	exp	13.8	38.0	26.2	78.0		0.90	$0.3 < P < 0.5$
44	obs	7	25	21	53	0.37		
	exp	7.3	24.7	21.0	53.0		0.01	$0.09 < P < 0.95$
45	obs	8	29	29	66	0.34		
	exp	7.6	29.6	28.7	65.9		0.03	$0.8 < P < 0.9$
46	obs	8	42	33	83	0.35		
	exp	10.2	37.8	35.1	83.1		0.84	$0.3 < P < 0.5$
47	obs	9	37	48	94	0.29		
	exp	7.9	38.7	47.4	94.0		0.23	$0.5 < P < 0.7$
48	obs	12	46	52	110	0.32		
	exp	11.3	47.9	50.9	110.1		0.14	$0.7 < P < 0.8$
49	obs	11	50	43	104	0.35		
	exp	12.7	47.3	43.9	103.9		0.41	$0.5 < P < 0.7$

Table 4. Observed distributions of transferrin groups in samples of sprat from the North Sea and Kattegat compared to expected Hardy-Weinberg distributions

Sample no.		Trasferrin groups			No.	q_A	χ^2	Probability of worse fit
		Tf AA	Tf AB	Tf BB				
50	obs	15	35	35	85	0.38		
	exp	12.3	40.1	32.7	85.1		1.40	$0.2<P<0.3$
51	obs	20	42	27	89	0.46		
	exp	18.8	44.2	26.0	89.0		0.23	$0.5<P<0.7$
52	obs	32	48	30	110	0.51		
	exp	28.6	55.0	26.4	110.0		1.79	$0.1<P<0.2$
54	obs	6	12	12	30	0.40		
	exp	4.8	14.4	10.8	30.0		0.83	$0.3<P<0.5$
55	obs	7	32	24	63	0.37		
	exp	8.6	29.4	25.0	63.0		0.57	$0.3<P<0.5$
56	obs	10	48	37	95	0.36		
	exp	12.3	43.8	38.9	95.0		0.92	$0.3<P<0.5$
57	obs	40	49	133	322	0.36		
	exp	41.7	48.4	131.9	322.0		0.08	$0.7<P<0.8$

3. The Kattegat samples coincided with part of the samples from western Norway, with most of the samples from the Skagerak coast and with one sample from the Oslo fjord. The samples from the North Sea also showed accordance with some of the samples from the Norwegian coast.
4. The present and previous analyses indicate that the sprat population in Norwegian waters consists of one major component recruited from Kattegat and the North Sea, and minor components recruited from local spawning in the fjords.

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I want to express my gratitude to several fishermen, to the staff of Neptun Canning Co., A/S Bergenhus Canning Co. and Noregs Sildesalgslag for help in obtaining samples. Likewise my thanks are due to director G. Dannevig, Statens Biologiske Stasjon Flødevigen, Arendal, for valuable discussion and encouragement and to the technical assistents who have carried out the analyses.

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Table I. Number of specimens analysed for hemoglobin and transferrin types in blood samples of sprat from western Norway (29—42), southeastern Norway (43—49), North Sea (50—54) and Kattegat (55—57).

Sample no.	Locality	Date	Hemoglobin	Transferrin	Age
29	Risnes, Masfj Hordaland	4 June 67	110	107	1-group
30	Skorpo, Hardangerfj, Hordaland	6 June 67	100	84	1-group
31	Gjermundshamn, Hordaland	6 June 67	88	55	1-group
32	Skorpo, Hardangerfj, Hordaland	6 June 67	104	94	1-group
33	Duesund, Masfj, Hordaland	12 June 67	123	124	1-group
34	Haveland, Sogn	19 June 67	105	101	1-group
35	Oppedalsøyra, Sogn	19 June 67	97	85	1-group
36	Lygrespollen, Hordaland	26 June 67	104	91	1-group
37	Lygrespollen, Hordaland	26 June 67	104	68	1-group
38	Tistam, Nordfjord	14 Oct. 67	78	82	1+2-group
39	Tistam, Nordfjord	14 Oct. 67	80	71	1+2-group
40	Borgenfjorden, Trøndelag	26 Oct. 67	62	40	0+1+2-group
41	Innvik, Nordfjord	26 June 68	93	56	1-group
42	Asgard, Austfj, Hordaland	12 Oct. 68	91	82	0-group
43	Bolærne, Oslofjorden	9 Sept. 68	50	78	1+2-group
44	Vollen, Oslofjorden	13 Sept. 68	55	53	1-group
45	Sandnesfj, Aust-Agder	29 Sept. 67	78	66	0-group
46	Bastøy Oslofjorden	30 Aug. 68	(91)	83	1+2-group
47	Husvik, Tønsberg Oslofjorden	30 Aug. 68	95	94	1+2-group
48	Flødevigen Aust-Agder	23 Oct. 68	120	110	0-group
49	Flødevigen Aust-Agder	25 Oct. 68	118	104	0-group
50	56°10′N, 05°25′E North Sea	24 Aug. 67	(120)	85	2-group
51	55°00′N, 06°00′E North Sea	28 Aug. 67	60	89	2-group
52	55°08′N, 03°32′E North Sea	29 Aug. 67	111	110	2-group

Table I (cont.)

Sample no.	Locality	Date	Hemoglobin	Transferrin	Age
53	53°19′N, 02°45′E North Sea	16 Sept. 67	82	—	2-group
54	58°21′N, 00°45′E North Sea	20 Sept. 67	112	30	2-group
55	57°35′N, 10°55′E Kattegat	8 Nov. 67	75	63	2-group
56	57°35′N, 10°55′E	8 Nov. 67	114	95	1-group
57	57°43′N, 10°50′E Kattegat	10 Nov. 67	321	322	2-group

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DISTRIBUTIONS OF MULTIPLE FORMS OF LACTATE DEHYDROGENASE, ASPARTATE AMINOTRANSFERASE AND SERUM ESTERASE IN HERRING FROM NORWEGIAN WATERS

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INTRODUCTION

Polymorphisms in the enzymes lactate dehydrogenase (LDH) and aspartate aminotransferase (AAT) of herring, *Clupea harengus*, were described by Odense, Allan and Leung (1966a, b). In LDH five different phenotypes were found. The LDH molecule consists of two kinds of monomers designated A and B under control by separate loci. The five different phenotypes represent two mutant alleles at the B locus and one at the A locus. In AAT two rare mutant alleles were observed.

Intraspecific variation both in weak and in strong components of serum esterase have been described, and the two groups of components were assumed to be controlled by genes at separate loci (Nævdal 1969).

The present paper deals with electrophoretic analyses of LDH and esterase phenotypes in herring samples from Norwegian waters, especially variation among samples from different localities. Analyses of AAT based on a limited material is reported.

MATERIAL AND METHODS

Sampling localities are shown in Fig. 1 and listed in Table 1 together with sampling dates, numbers of specimens in each sample and other available data. Fig. 1 also shows sampling localities of the samples (no. 1—10) previously analysed for serum esterase (Nævdal 1969). The results of these analyses are included in the following discussion.

LDH types were determined from analyses of sera in samples numbered 10—15 and 20, and from muscle extract in the other samples. Sample 19 was analysed for AAT types from muscle extract. Analyses of esterase were performed on all samples of which sera were available.

Combined starch and agar gel electrophoresis (Møller 1966) for three hours was carried out to reveal the LDH types and for two hours to reveal the AAT types. The zones of enzyme activity were stained as

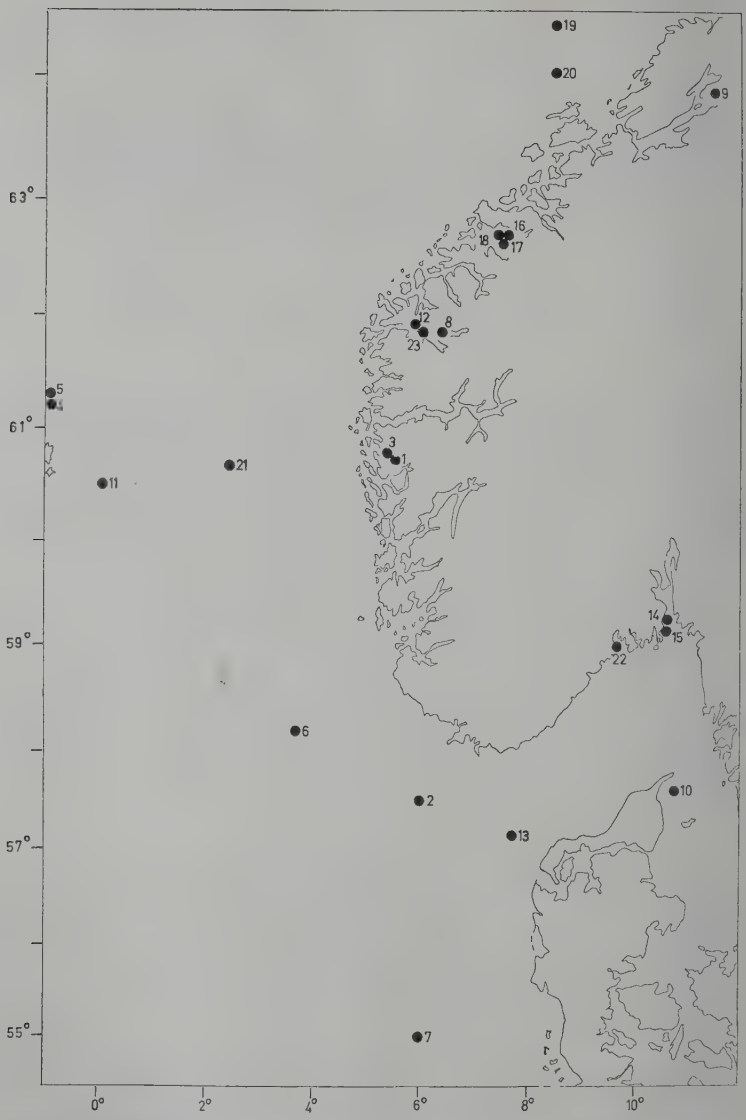

Fig. 1. Sampling localities of blood samples of herring from the Norwegian coast and the North Sea.

Table 1. Distribution of LDH phenotypes in samples of herring from the Norwegian coast and the North Sea.

Sample no.	Locality and date of sampling	Indications of sample	LDH phenotypes AABB	AABB′	AAB′B′	AABB″	AA′BB	No.	Gene frequency B′	B″	A′
11	60°31′N, 00°05′E North Sea, 19—20 June 68	Adult autumn spawners	81	11	1	—	—	93	0.07	—	—
12	Eid, Nordfjord, 1 July 68	1-group	93	4	—	—	—	97	0.02	—	—
13	57°10′N, 07°40′E, North Sea, 2 Aug. 68	Immature autumn spawners	76	9	1	—	—	86	0.06	—	—
14	Bastøy, Oslofjorden, 30 Aug. 68	Immature, about 20 cm	113	9	—	—	—	122	0.04	—	—
15	Nøtterøy, Oslofjorden, 30 Aug. 68	0-group	72	5	—	—	—	77	0.03	—	—
16	Langfjorden, Romsdal, 21 Sept. 68	0-group	102	18	—	—	—	120	0.08	—	—
17	Langfjorden, Romsdal, 21 Sept. 68	Immature, 13—16 cm	86	11	—	—	—	97	0.06	—	—
18	Langfjorden, Romsdal, 21 Sept. 68	Immature, 16 cm	91	8	—	—	—	99	0.04	—	—
19	64°25′N, 08°25′E, off Trøndelag, 20 Feb. 69	Norwegian spring spawners	92	7	1	—	—	100	0.05	—	—
20	64°02′N, 08°25′E, off Trøndelag, 26 Feb. 69	Norwegian spring spawners	196	20	1	—	—	217	0.05	—	—
21	60°40′N, 02°30′E, North Sea, 24 March 69	Mainly autumn spawners	88	5	1	1	—	95	0.04	0.005	—
22	Langesundsfjorden near Porsgrunn, 26 March 69	Adult spring	87	6	—	1	1	95	0.03	0.005	0.005
23	Ålfoten, Nordfjord, 2 June 69	Immature	131	25	—	—	—	156	0.08	—	—

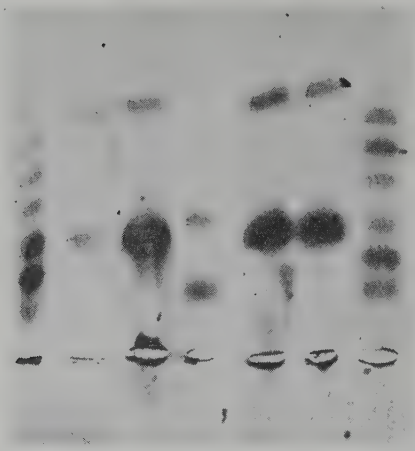

Fig. 2. Photograph of herring lactate dehydrogenase activity after combined starch and agar gel electrophoresis at pH 9.0 for three hours. From left to right the types are BB′, BB, BB, B′B′, BB, BB, and BB′.

described by Odense *et al.* (1966a, b). Analyses of esterase were carried out as described previously (Nævdal 1969).

RESULTS AND DISCUSSION

Patterns similar to the LDH phenotypes described by Odense *et al.* (1966a, b) were found in the present material (Fig. 2), and they were interpreted to represent the same genotypes. The observed LDH phenotypes were named AABB, AABB′, AAB′B′, AABB″ and AA′BB by Odense *et al.* (1966a, b), where B′ and B″ represent mutant alleles at the B locus and A′ represent a mutant allele at the A locus. The LDH components were well separated by the present method and the phenotypes usually easily recognized. The distributions of the phenotypes are given in Table 1.

Muscle extract showed stronger LDH activity than sera, and all specimens could be determined for LDH phenotypes from muscle extract. When sera were analysed a few specimens of some samples could not be determined due to the weakness of the zones, and thus the numbers of specimens determined for LDH types were lower than the numbers determined for esterase types in some samples. When stored frozen the LDH activity of sera was reduced considerably after a few weeks while it persisted for at least half a year in muscle.

Of the 100 specimens analysed for AAT types two showed a three band pattern which was interpreted as the phenotype SS′ of Odense *et al.* (1966 a, b) while all the others showed a one band pattern, probably the one named SS (Fig. 3).

Table 2. Observed distributions of esterase phenotypes in herring, compared with expected distribution according to the Hardy-Weinberg law.

Sample no.	Types of weak esterase zones					Types of strong esterase zones								
	Es m_1m_1	Es m_1m_2	Es m_2m_2	No.	q_1	Es FF	Es FM	Es MM	Es MS	Es MS_2	No.	q_F	qs_1	qs_2
11 obs.	87	8	—	95	0.96	—	6	90	—	—	96	0.03	—	—
exp.	87.6	7.3	0.2			0.1	5.6	90.3	—	—				
12 obs.	67	12	1	80	0.91	1	16	83	—	—	100	0.09	—	—
exp.	66.2	13.1	0.6			0.8	16.4	82.8	—	—				
13 obs.	81	10	3	94	0.91		3	103	—	—	106	0.01	—	—
exp.	77.8	15.4	0.8			0.01	2.9	103.1	—	—				
14 obs.	106	14	1	121	0.93	—	1	123	—	—	124	0.004	—	—
exp.	104.7	15.8	0.6			0.0	1.0	123.0	—	—				
15 obs.	68	2	1	71	0.96	—	1	79	—	—	80	0.01	—	—
exp.	65.4	5.5	0.1			0.01	1.6	78.4	—	—				
16 obs.	40	21	3	64	0.79	5	16	72	—	—	93	0.14	—	—
exp.	39.9	21.2	2.8			1.8	22.4	68.8	—	—				
17 obs.	51	31	5	87	0.76	4	11	87	2	—	104	0.09	0.01	—
exp.	50.3	31.7	4.9			0.8	16.8	84.2	1.9	—				
18 obs.	69	16	6	91	0.85	—	11	89	—	—	100	0.06	—	—
exp.	65.7	23.2	2.0			0.4	11.3	88.3	—	—				
20 obs.	183	88	9	280	0.81	1	15	276	3	1	296	0.03	0.01	0.002
exp.	183.7	86.2	10.1			0.3	17.0	274.5	2.8	1.1				
23 obs.	139	16	3	158	0.93	1	3	152	3	—	159	0.02	0.01	—
exp.	136.7	20.6	0.8			0.04	5.0	150.8	3.1	—				

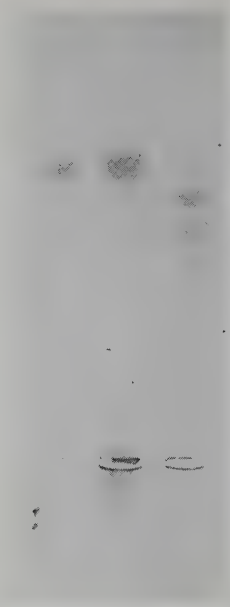

Fig. 3. Photograph of herring aspartate aminotransferase activity after combined starch and agar gel electrophoresis at pH 9.0 for two hours. From left to right the types are SS, SS, and SS′.

Comparing the results of the present study with corresponding results from the West Atlantic (Odense *et al.* 1966a, b), the B′ gene seems to be somewhat more frequent on the European side while the S′ gene seems to occur at about the same frequency on both sides of the Atlantic as far as can be stated from the present material. The LDH genes B″ and A′ were found only in two and one specimens respectively, and the AAT gene S″ were not found at all in the samples from Norwegian waters. They were also very rare in the samples from the West Atlantic.

Distributions of esterase phenotypes are shown in Table 2. Relatively good accordance between observed distributions and expected Hardy-Weinberg distributions were found, but in some samples there was an excess of hypothetical homozygotes. This may be caused by mixing of individuals from populations which differ in frequencies of the esterase controlling genes. The hypothesis of genetical control (Nævdal 1969) still seems to be valid, but modifications or other explanations cannot be excluded.

Several bands in the region of the Es m_1 and Es m_2 components were indicated on some electrophoretograms, but they showed only small differences in electrophoretic mobility, and separation into more phenotypes is hardly possible by the present method. Distinction between the m_1 and m_2 phenotypes only is therefore a simplification which may reduce the reliability of the type determinations. In addition the weakness of the components may cause errors. However, differences of the order observed among some of the present samples (see below) cannot be explained as a result of incorrect type determinations alone. Due to the weakness of the zones the numbers of specimens determined for m_1m_2 types were often lower than the numbers determined for types of strong esterase components and LDH.

Tables 1 and 2 show that variations in frequency distributions of phenotypes among samples occurred in both groups of esterase and in

LDH. The significance of these variations have been tested by χ^2-homogeneity tests. The results of the previous analyses (Nævdal 1969) of samples numbered one to ten are included in the tests.

Among the total samples the variations were significant at the one per cent level in both groups of esterase while the variations in distributions of LDH phenotypes were insignificant.

When treating the samples of North Sea autumn spawners separately, the differences in distributions of the types of weak esterase zones were found to be significant while the variations in distributions of types of strong esterase components and LDH types were insignificant. This variation was largely contributed to by sample 7 which were collected at Bløden Ground and probably represent the Down herring stock while the other samples more likely represent either the Bank herring or Kattegat autumn spawners (Haraldsvik 1969). Sample 10, collected in Kattegat, deviated from the North Sea samples with regard to distributions of types of strong esterase zones (low numbers of specimens prevented statistical tests), but not in types of weak esterase components.

All specimens in sample 5 of North Sea spring spawners were of the Es m_1m_1 phenotype, and the sample contained one specimen with the rare Es S_2 component. However, the small numbers of specimens in this sample prevented further conclusions. Unfortunately, analyses of LDH phenotypes were not undertaken on the first ten samples.

When treating the samples collected from inshore waters separately, the variation among samples was found to be significant at the one per cent level in distributions of types of both groups of esterase, and at the 5 per cent level in distribution of LDH phenotypes. Some samples coincided with the North Sea samples (for instance no. 14 and 15 from the Oslo fjord) or with samples from Norwegian spring spawners (for instance no. 18) while others showed frequency distributions not found in samples from offshore waters. No marked geographical trend could be seen in the variations. The results indicate that the herring in Norwegian inshore waters may be recruited both by immigration from offshore waters (by drift of larvae or by active immigration) or from local spawning, and that herring in these areas, especially the small herring, may represent different groups in different years and areas. However, for a complete account of the herring stocks in inshore waters and the origin of the young herring which occur in the fjords, the present material is too limited.

It may be concluded that the present study on herring enzymes has shown that among groups of herring in Norwegian waters and in the North Sea significant variations exist in characteristics which probably are genetically controlled and not affected by environmental factors.

SUMMARY

1. By use of combined starch and agar gel electrophoresis 10 samples (1258 specimens) were studied for serum esterase polymorphism, 13 samples (1454 specimens) for lactate dehydrogenase (LDH) polymorphisms and one sample (100 specimens) for asparate aminotransferrase (AAT) polymorphism.

   The samples were collected in Norwegian waters and the North Sea.
2. In two groups of esterase (weak and strong components) and in LDH and AAT intraspecific, hereditable variations were observed.
3. Frequencies of LDH and AAT phenotypes were found to be similar to corresponding frequencies observed in samples from Canadian waters.
4. Statistically significant variations among samples were observed in distributions of the phenotypes, especially the esterase phenotypes.

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STUDIES ON BLOOD PROTEINS OF MACKEREL

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INTRODUCTION

The mackerel, *Scomber scombrus*, spawns in the northeastern North Sea and Skagerak, and another spawning area is located south of Ireland. Tagging experiments (Bolster 1962, 1965, Revheim, personal communication) have shown that interchange of individual mackerel takes place between the two main spawning areas, but it is still not known whether the two main spawning stocks consist of two (or more) separate population units or whether the mackerel within these areas should be regarded as one single unit.

The present paper deals with studies on hemoglobins, serum proteins and serum esterase for the purpose of identifying characteristics to be applied on the population problems of mackerel.

The results of the studies on serum esterase have been dealt with in a separate report (Jamieson, de Ligny and Nævdal 1969) where also the results of the present study have been compared to corresponding results of samples from the southern North Sea and the waters south of Great Britain and Ireland.

MATERIAL AND METHODS

Sampling and treatment of mackerel samples were made as described for herring and sprat (Nævdal 1968, 1969). No anticoagulant was used because the mackerel blood clotted only partly, and hemolysate could easily be prepared. The hemoglobins were analysed fresh, but because of hard working stress at the laboratory at certain periods, some serum samples had to be stored in the deep freeze for some weeks before the analyses could be carried out.

The hemoglobins were analysed by the agar gel electrophoresis described by Sick (1965) for 60 minutes. The sera were analysed in combined starch and agar gel electrophoresis (Sick 1965, Møller 1966). For separation of serum proteins and esterase components 90 minutes were found to be sufficient. When analysing esterase, three sera were

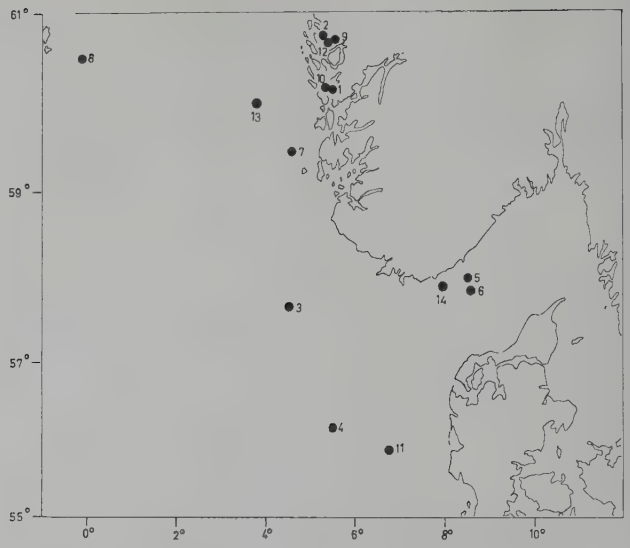


Fig. 1. Sampling localities of blood samples of mackerel.

run on each slide, the middle one being a reference serum of known type.

Staining of proteins and esterase bands, and identification of transferrins and haptoglobins were carried out as for similar studies on sprat (Nævdal 1968, 1969). Only samples collected in 1967 and later were analysed with respect to esterase phenotypes.

Sampling localities, date of sampling and other data of the samples are listed in Table I. Fig. 1 shows the sampling localities.

To see whether the results of the analyses of esterase phenotypes obtained by the present method corresponded to the results by starch gel electrophoresis, sera have been exchanged with other laboratories, and the electrophoretograms have been carefully compared (Jamieson *et al.* 1969).

RESULTS AND DISCUSSION

HEMOGLOBINS

The hemoglobins of the mackerel moved towards the cathode in agar gel at pH 7.3 with a mobility in the range of several other fish species, for instance herring and sprat (Wilkins and Iles 1966), cod (Sick 1965) and some other gadoids (Møller and Nævdal 1969). The hemoglobin patterns found in mackerel are shown in Fig. 2.

The Hb component of lowest cathodic mobility, named HbII, was

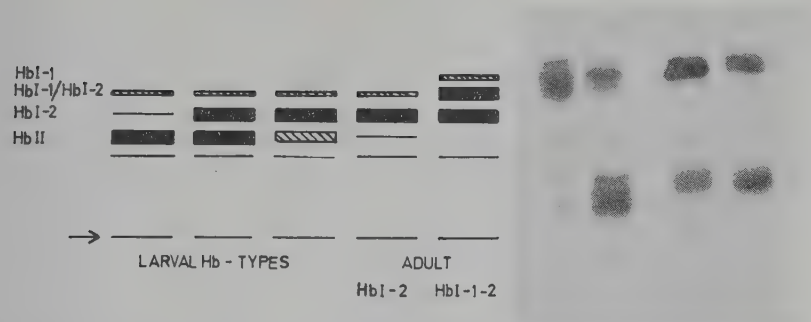


Fig. 2. Outline of hemoglobin patterns in mackerel by agar gel electrophoresis at pH 7.2 and photograph of electrophoretograms from routine analyses. The left part of the photograph are patterns of 0-group mackerel, and the right part are patterns from adult. Filled in bars: strong bands. Hatched bars: moderately strong bands. Single lines: faint bands. Arrow indicates the point of application.

found in samples 1 and 2 of the 0 group. Also in these samples the HbII component varied in strength. In some specimens HbII was the only strong component (left pattern in Fig. 2) while it was nearly absent in others. Sample 12, which also represented the 0-group, showed only weak traces of the HbII component. This sample, collected in October, contained fishes of about 23 cm in length (extremely high growth rate) while samples 1 and 2 represented fishes of 10—12 cm in length. In older fishes only faint traces of the HbII component were seen. Although several length stages were not represented in the present material, it is evident that the ontogenetic variation of the HbII component depend on growth or length rather than on age. However, the ontogenetic variation is less pronounced than in salmon, *Salmo salar*, (Kock, Evans and Bergstrøm 1966) and herring, *Clupea harengus*, (Wilkins and Iles 1966) where it was found to persists up to significantly older stages in the fish's life.

In mackerel, one year and older, two strong components were found. The component of highest cathodic mobility, named HbI-1, was only present in a few specimens while the other, named HbI-2, was present in all specimens analysed. Thus two phenotypes, named HbI-1-2 (containing both components) and HbI-1 (containing only the component HbI-1) were found. Weak components were seen at the cathodic side of HbI-1 and HbI-2 (named HbI-1′ and HbI-2′ respectively). The HbI-1′ and HbI-2′ components may correspond to weak components of the same designation in cod, *Gadus morhua*, (Sick 1965), sprat, *Sprattus sprattus*, (Nævdal 1968) and other fishes (Møller and Nævdal 1969). They surely increased upon storing, but were also

present in completely fresh material, and HbI-2′ was found in the hemoglobin pattern of 0-group mackerel even when HbI-2 was seen only as a faint band. Often HbI-2′ was stronger in the 0-group than in older fishes.

As a hypothesis the components HbI-1 and HbI-2 are controlled by two co-dominant alleles, *HbI*^{1} and *HbI*^{2}. The expected genotype represented by a phenotype with HbI-1 as the only strong component was not found, but because of the scarsity of the hypothetical gene *HbI*^{1} it should not be expected in the present material. Accordingly, both ontogenetic and genetically controlled variations seem to be present in mackerel hemoglobins. The genetically controlled variation may potentially be used for studies on population units, but in mackerel one of the hypothetical hemoglobin-controlling genes, *HbI*^{1}, is so rare that the variation is of little value for this purpose.

SERUM PROTEINS

All serum proteins moved towards the anode in combined starch and agar gel electrophoresis at pH 9.0. The electrophoretograms obtained are outlined in Fig. 3.

In front of the albumins was seen a moderately strong component, followed at its cathodic side of a weaker one. By the present method intranspecific variations could not be detected in these components or in the albumins.

The transferrins were located near the albumins at their cathodic side. This high anodic mobility of transferrins conforms with the mobility of transferrins of some flat fishes (DE LIGNY 1967) while the transferrins of several other fishes have been found to possess a much lower anodic mobility (MØLLER 1966, MØLLER and NÆVDAL 1967).

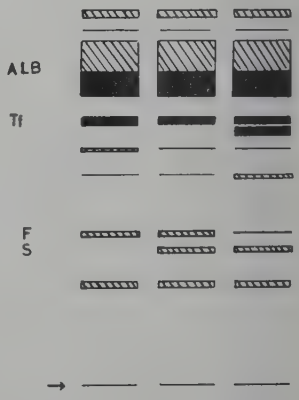


Fig. 3. Outline of serum protein patterns of mackerel by combined starch and agar gel electrophoresis at pH 9.0. Legend: see Fig. 2.

In most adult specimens only one band representing transferrins were found, but in a few specimens another strong band occurred at its catodic side. (Fig. 3). This rare band could not be tested autoradiographically since sera in which it occurred were not available when the tracing experiments were made. Its strength and position, however, suggests that it represents a rare transferrin component which may be

genetically controlled, but it is too rare to be utilized for studies on population units.

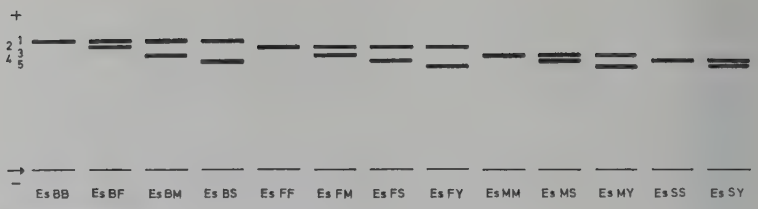
Another component was frequently seen at the anodic side of the common transferrin band in sera of 0-group mackerel and sometimes also in sera of older but immature fishes. The relative intensity of the two bands varied, and in some specimens the cathodic component (the common transferrin in adults) was nearly absent. Evidently these variations were related to ontogeny and therefore of no use for population unit studies.

Behind the transferrins two or more components were located. These components varied both in location and strength, and were often diffuse and very weak, but occasionally strong. These variations were not clear enough to form the basis of proper classification of the specimens.

One or both of the moderately strong components of unknown nature, tentatively named F and S, occurred in each specimen. Consequently three phenotypes, named FF, FS and SS, might be distinguished. Presence of faint bands at the positions of the lacking ordinary F or S band (Fig. 3), however, complicated the classification of the specimens, and the phenotypes did not seem to be completely stable because the intensity of the faint bands varied among repeated analyses of the same sera. A hypothesis of control by two allelomorphic genes was introduced and gene frequencies and expected Hardy-Weinberg distributions were calculated. In most samples there was fairly good accordance between observed and expected distributions, and gene frequencies (q_F) showed approximately the same values. However, samples 11 and 12, both from young mackerel, showed considerably lower q_F values, and sample 12 also showed slight accordance between observed and expected distributions. Because it seems unlikely that the samples from young mackerel should represent other population units than the rest of the samples, and because of the unstability of the phenotypes, frequencies of the present characteristics are doubtful as parameters for studies of population units.

The band located at the cathodic side of the component named S, represent haptoglobins. It increased in strength when hemoglobins were added to the sera, and it stained with o-dianisidine. The free hemoglobins also moved towards the anode by the present method, but with a mobility lower than any of the serum proteins.

Although variations in several groups of serum proteins of mackerel have been observed by the present methods, none of these variations seem at present to be useful for studies of population units of this species.



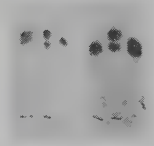


Fig. 4. Outline of serum esterase patterns in mackerel by combined starch and agar gel electrophoresis at pH 9.0, and photograph of electrophoretograms from routine analyses. From left to right the photographed patterns are: Es FM, Es FS, Es MM, Es SS, Es FS, and Es MS. Legend: see Fig. 2.

SERUM ESTERASE

Several components which represented esterase activity could be distinguished. But only small differences in electrophoretic mobility were observed among some of the components, and therefore they could not all form the basis of proper classification of the specimens. For this reason they were combined into five main components named Es B, Es F, Es M, Es S and Es Y in order of decreasing anodic mobility. One or two of these main components were present in each specimen, and the phenotypes got their designations according to the components they possessed, i.e. specimens with only Es B were said to belong to the phenotype Es BB, specimens with both Es B and Es F to the phenotype Es BF, etc. Of the 15 possible combinations, 13 were found. The observed phenotypes are outlined in Fig. 4.

A hypothesis of control by a series of polyalleles was introduced to explain the esterase variation. The alleles were named Es^{B}, Es^{F}, etc. according to the esterase component they were supposed to control. Table 1 gives observed distributions of esterase phenotypes together with calculated gene frequencies and expected Hardy-Weinberg distributions.

Significant deviations between observed and expected distributions were found in samples 5, 6, 7 and 14 where a clear excess of hypothetical homozygotes was observed. Also in the other samples, except sample 11, an excess of homozygotes was noted, but the overall accordance between observed and expected distributions was rather good.

The samples which showed the greatest deviation between observed and expected distributions were all sampled from adult fishes near spawning or in spawning condition. However, this tendency was not clear because for instance sample 12, which was sampled from the 0-group, also showed considerable deviation from expected distribution.

Table 1. Distributions of esterase phenotypes in mackerel samples from the North Sea and the Norwegian coast. obs: observed distributions, exp: expected Hardy-Weinberg distributions.

Sample no.	Esterase phenotypes													No.	Gene frequencies				
	BB	BF	BM	BS	FF	FM	FS	FY	MM	MS	MY	SS	SY		q_B	q_F	q_M	q_S	q_Y
4 obs	—	—	—	—	7	20	5	—	19	4	—	—	—	55	—	.355	.564	.082	—
exp.	—	—	—	—	6.9	22.0	3.2	—	17.5	5.1	—	0.4	—						
5 obs.	—	—	2	—	18	27	6	—	40	18	—	1	—	112	.009	.308	.567	.116	—
exp.	0.0	0.6	1.1	0.2	10.6	39.1	8.0	—	36.0	14.7	—	1.5	—						
6 obs.	—	1	2	—	32	60	6	2	84	24	2	3	—	216	.007	.308	.593	.083	.009
exp.	0.0	0.9	1.8	0.3	20.5	78.9	11.0	1.2	76.0	21.3	2.3	1.5	0.3						
7 obs.	—	—	6	1	33	59	14	—	109	15	1	4	—	242	.014	.287	.618	.079	.002
exp.	0.0	1.9	4.2	0.5	19.9	85.8	11.0	0.3	92.4	23.6	0.6	1.5	0.1						
8 obs.	—	—	—	—	3	11	3	—	16	5	1	—	—	39	—	.256	.628	.103	.013
exp.	—	—	—	—	2.6	12.5	2.1	0.2	15.4	5.0	0.6	0.4	0.1						
9 obs.	—	1	2	—	11	24	7	2	46	11	—	—	1	105	.014	.267	.614	.090	.014
exp.	0.0	0.8	1.8	0.3	7.5	34.4	5.0	0.8	39.6	11.6	1.8	0.9	0.3						
10 obs.	—	—	2	1	11	30	5	—	39	9	1	1	—	99	.015	.288	.606	.086	.005
exp.	0.0	0.9	1.8	0.3	8.2	34.6	4.9	0.3	36.4	10.3	0.6	0.7	0.1						
11 obs.	—	1	3	—	7	44	4	—	33	11	—	1	1.1	105	.019	.300	.590	.086	.005
exp.	0.0	1.2	2.4	0.3	9.5	37.2	5.4	0.3	36.6	10.7	0.6	0.8	0.1						
12 obs.	—	1	4	—	12	24	3	—	42	12	—	2	—	100	.025	.260	.620	.095	—
exp.	0.1	1.3	3.1	0.5	6.7	32.2	4.9	—	38.4	11.8	—	0.9	—						
13 obs.	1	2	10	—	41	96	18	—	95	31	1	3	3.1	299	.024	.331	.548	.094	.003
exp.	0.2	4.8	7.9	1.3	32.8	108.5	18.6	0.6	89.8	30.8	1.0	2.6	0.2						
14 obs.	1	2	6	1	17	33	10	1	65	9	1	1	—	147	.037	.272	.609	.075	.007
exp.	0.2	3.0	6.6	0.8	10.9	48.7	6.0	0.6	54.5	13.4	1.3	0.8	0.1						

Sampling of mixed populations, selection against heterozygotes (*negative heterosis*), or methodical error may be reasons for the deviations between observed and expected distributions. However, excistence of populations with different value of gene frequencies was not indicated by the results of any of the analysed samples. Negative heterosis has been observed in some cases of protein polymorphism (Manwell and Baker 1969), but should be expected to affect all samples to the same degree. Methodical error might rise because the two bands of the hypothetical heterozygotes sometimes appeared very different in strength. In specimens of generally weak esterase activity the weaker band might be overlooked, and heterozygotes might be classified as homozygotes. However, all specimens were analysed at least twice, and weak bands were carefully looked for. Therefore it seems improbable that this type of error could account for the observed deviations.

Thus no satisfactory explanation of the deviations between observed and expected distributions in some of the samples can be given. The hypothesis of genetical control, however, is supported by the comparatively good accordance in the other samples. In some tuna species genetically controlled variations in serum esterase were found (Sprague 1967, Fujino and Kang 1968). The resemblance between the esterase variations of tuna and of mackerel also supports the introduced hypothesis. Consequently, the hypothesis seems reasonable, and the observed gene frequencies may be regarded as characteristic sample parameters.

No marked differences in observed gene frequencies were observed among the samples, and the results of the present study give no reason to believe that more than one population unit of mackerel inhabit the area from which samples were collected. The gene frequencies did not deviate clearly from corresponding results of samples from the southern North Sea and the area south and west of Ireland (Jamieson *et al.* 1969), and therefore the studies on serum esterase have given no indications of separate population units in the North Sea and west and south of the British Islands.

SUMMARY

1. 14 samples of mackerel, about 1800 specimens, from the North Sea and the Norwegian Coast were analysed by agar gel electrophoresis (hemoglobins) and combined starch and agar gel electrophoresis (serum proteins and serum esterase).
2. Hemoglobin variations related to ontogeny appeared during the first year of the mackerel's life. In mackerel one year and older normally one strong hemoglobin component occurred. Two strong components

were observed in some specimens (probably heterozygotes) but too infrequently to be used for studies on population units.

3. In the serum proteins were found extensive variations, but the greater part of the variations occurred in very weak bands, or the observed phenotypes were somewhat unstable. Normally one transferrin band was seen, but also a double band pattern (probably heterozygote) were observed although too infrequently to be used in studies of population units.
4. Five esterase components could be clearly distinguished, and a few more were indicated. Each of the components seemed to be controlled by one gene in a series of polyalleles, although some samples showed a significant excess of observed homozygotes according to this theory.
5. No significant variations in gene frequencies between the samples were found. The results also were approximately in accordance with corresponding results from the southern North Sea and the areas south of the British Islands.

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Table I. Number of specimens analyzed for hemoglobins, serum proteins and serum esterase in blood samples of mackerel from the Norwegian coast and the North Sea.

Sample no.	Locality and date	Indications of sample	Hemoglobin	Serum proteins	Esterase
1	Håvik i Fusa, Hordaland, 5 Oct. 65	0-group	33	30	—
2	Fensfjorden, Hordaland, 15 Oct. 65	0-group	28	25	—
3	57°40′N, 04°30′E, North Sea, 25 May 66	Adult, near spawning	99	88	—
4	56°10′N, 05°30′E, North Sea, 25 Aug. 67	Mixed	85	40	55
5	57°58′N, 08°14′E, North Sea, 28 May 68	Adult, near spawning	120	103	120
6	57°55′N, 08°20′E, North Sea, 29 May 68	Adult, near spawning	225	207	215
7	59°27′N, 04°40′E, North Sea, 12 June 68	Adult, spawning	274	177	242
8	60°31′N, 00°05′E, North Sea, 20 June 68	Immature	40	30	39
9	Stall, Austfj., Hordaland, 1 July 68	Adult, spawning	110	75	105
10	Vernøy, Bjørnefj., Hordaland, 13 July 68	Adult, spawned	100	99	88
11	55°50′N, 06°45′E, North Sea, 9 Aug. 68	Immature	90	70	105
12	Asgard, Austfj., Hordaland, 12 Oct. 68	0-group	100	99	100
13	60°00′N, 03°50′E, North Sea, 24 April 69	Mixed, mainly immature	300	272	299
14	57°56′N, 08°00′E, North Sea, 10 June 69	Adult, near spawning	200	—	147

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